Fecundity, seed dispersal and seedling growth dynamics of common deciduous tree species at Wytham Woods, UK

Thesis by

Zetian Liu

Submitted in partial fulfilment of the requirements of the Degree of

Doctor of Philosophy

Queen Mary, University of London
2018
(Submitted September 21, 2018)

Statement of originality

I, Zetian Liu, confirm that the research included within this thesis is my own work or that where it has been carried out in collaboration with, or supported by others, that this is duly acknowledged below and my contribution indicated. Previously published material is also acknowledged below.

I attest that I have exercised reasonable care to ensure that the work is original, and does not to the best of my knowledge break any UK law, infringe any third party's copyright or other Intellectual Property Right, or contain any confidential material.

I accept that the College has the right to use plagiarism detection software to check the electronic version of the thesis.

I confirm that this thesis has not been previously submitted for the award of a degree by this or any other university.

Signature:

Date: 01/09/2018

Details of collaboration and publications:

This work has not been published by the submission date of

the thesis.

Acknowledgements

First, I would like to express my deep gratitude to my supervisors: Professor Mathew Evans and Professor Andrew Leitch for their invaluable guidance and patience.

Huge thanks to Dr Lili Wang for help coding SORTIE functions used in the thesis. Many thanks to Dr Aris Moustakas and Dr Richard Buggs for their helpful advices. I am grateful to the Oxford University for allowing me to research at the Wytham Woods.

I would like to thank my friends at School of Biological and Chemical Sciences: Liu Yu, Nana, Wencai, James and Feifan for their help and support.

I wish to express sincere thanks to my family for their unceasing support.

Financial support was provided by the China Scholarship Council and Queen Mary, University of London.

Abstract

Processes such as seed production, dispersal and seedling establishment are important in shaping forest species composition and maintaining species diversity. These processes allow trees to colonize new regions and are critical in determining tree species' responses to ongoing climate change and resulting changes in forest structure and composition. It is important to gain knowledge of tree regeneration processes to better understand the biological responses to environmental changes. Predictive forest models with of explicit regeneration processes will more accurately predict forest dynamics in response to climate change, habitat fragmentation and other environmental changes. In my PhD I studied three vital components of regeneration: seed production and dispersal, seedling growth and seedling survival, with field data collected at Wytham Woods, UK. The studied species are common deciduous tree species of UK woodlands: Ash (*Fraxinus excelsior* L.), Beech (*Fagus sylvatica* L.), Birch (*Betula spp*.) and Sycamore (*Acer pseudoplatanus* L.). In this thesis, I (1) estimated seed production from mature trees and developed a seed dispersal kernel to explore the effects of surrounding environment on seed production and dispersal; (2) estimated the relationship between light intensity and seedling diameter growth, and; (3) studied the effects of light, seedling size and herbivore browsing on seedling survival. The results characterized differences in patterns of regeneration between the studied species. Furthermore, these modelled processes were incorporated into an individual based predictive forest model "SORTIE" calibrated for Wytham Woods, UK. The model was run for 80 simulated years. Compared with a model without explicit seedling regeneration processes, but which initiates new trees as saplings, the model predicted similar adult tree species composition but resulted in significantly more trees and different spatial distribution patterns. The data show that incorporation of regeneration processes starting from seed production can have important impact on the predictions of models. Future studies, which relate regeneration with climate change, will provide valuable insights on predicting forest dynamics.

Table of Contents

List of Tables

List of Figures

Chapter 1 General Introduction

Forest regeneration

Forest ecosystems are amongst the most important ecosystems in the world. They provide valuable products like fuel, timber and recreation (Patterson and Coelho 2009). Forests are major carbon pools and play an important role in regulating the carbon cycle, as well as providing other critical ecosystem services like soil erosion control, improving air quality, and regulating rainfall (Schimel 1995, Krieger 2001). In addition forests are well known for supporting high biodiversity, with tropical forests estimated to be home to two thirds of terrestrial biodiversity (Krieger 2001).

Climate change, deforestation, and biological invasions are all posing threats to forest biodiversity and integrity, and change in forest structure and functions in various ways (Overpeck et al. 1990, Schröter et al. 2005, Tubby and Webber 2010). For example, there are increasing numbers of exotic pathogens that are causing declines in the abundance of common trees, greatly altering forest community composition (Brasier 1979, Pautasso et al. 2013). In addition climate change is resulting in increasing frequencies of prolonged drought in some areas, which will likely affect tree dominance, depending on drought resistance (Valladares and Niinemets 2008, Cavin et al. 2013) . Changes in tree communities will cascade into associated biodiversity and ecosystem functions (Schröter et al. 2005). Understanding forest dynamics is critical to forest management and conservation, which are facing unprecedented challenges in a time of global change. The recruitment of trees is key to the persistence of a forest, it has a huge effect on forest dynamics, and is prone to be affected by changes of environment (Grubb 1977, Clark et al. 1999a). Therefore, understanding tree regeneration is particularly important to inform the conservation and management of forests.

Regeneration of trees is defined as the process by which new tree individuals replace mature individuals via seed production, dispersal, germination, seedling establishment (Grubb 1977). Regeneration allows trees to renew their populations and colonize unoccupied habitats,

shaping the distribution of forest trees, and driving plant population and community dynamics (Grubb 1977, Denslow 1987, Howe and Miriti 2004). Many researchers believe differences in regeneration success are crucial to community species composition and species coexistence (Nakashizuka 2001, Silvertown 2004, Myers and Harms 2009). Mature trees are generally long-lived and seed to seedling stages only account for a small part of a tree's life cycle, but seeds and juvenile trees are more vulnerable to changes in environmental conditions and most mortality happens at these stages (Moles and Westoby 2004). Processes at early life stages are considered to have disproportionate influence to population and community (Clark et al. 2007, Larson and Funk 2016). Each stage from seed production to seedling establishment is a distinctive process and affected by a combination of different abiotic and biotic factors. Therefore the understanding of regeneration needs knowledge from various life-stages and their roles in regeneration to be combined. (Clark et al. 1998b).

The importance of different environmental requirements of trees during their regeneration stages have been subject of studies for a long time. For example, foresters and scientists have long noticed contrasting shade tolerance of juvenile trees, and differences influence forest succession (Shugart 1984, Kobe et al. 1995). Based on this, the classic regeneration niche partitioning theory suggests that differences in regeneration niches is the reason why large number of plant species can coexist, especially in tropical forests (Grubb 1977, Denslow 1987).

Each regeneration stage is affected by different extrinsic and intrinsic factors. For a tree species, failure over any of the regeneration stages would pose limitations on its recruitment. Clark et al. (2007) classified recruitment limitation of trees into seed limitation and establishment limitation. Seed limitation is related to seed production and dispersal and happens when there is lack of productive adult trees to produce enough seeds or seeds fail to arrive at suitable recruitment sites (Clark et al. 1998c). Establishment limitation can occur during various processes from seed germination to seedling establishment after seeds are

deposited. Factors which determinate establishment limitation are usually environmental conditions of microsites (Turnbull et al. 2000, Pearson et al. 2002).

Seed production and dispersal

Seed production

Seed production is a complicated processes and accurate predictions are difficult to make, because direct observations of seed production from individual trees are problematic. Consequently most data are collected at the population level (Herrera et al. 1998, Clark et al. 2004). The production of seeds is an important ecological process, not only for the persistence of tree populations, but also to the population demography of animals feeding on seeds (Hannon et al. 1987, Jones et al. 1998). The number of seeds produced is considered an evolutionary trait related to other traits like seed size and dispersal distance. A classical hypothesis is that trade-off exists in plants between producing a large number of small seeds versus producing a small number of large seeds (Tilman 1994, Clark et al. 2004, Moles and Westoby 2006). This hypothesis is based on the assumption that large seeds have higher reserves and thus they have higher survival probabilities and competition capacities at the seedling stage, while small seeds have longer dispersal distances and can occupy more suitable sites with large numbers per site. To some extent, existing data confirms that this hypotheses is correct : Small seeded plants do have higher annual seed production, and they also have shorter life spans and reproductive years (Moles et al. 2004). The survival advantage of large seed species have been validated at the early stages after seedling establishment (Leishman 2001, Moles and Westoby 2006). The negative relationships between dispersal distance and seed size have also been found in several tropical and temperate tree communities (Greene and Johnson 1989, Muller-Landau et al. 2008). Nevertheless, a more recent and comprehensive meta-analysis shows that seeds size only has weak or little effect on dispersal distance across species (Thomson et al. 2011).

It has been long recognized that many tree species have high annual variation in seed production (Harmer 1994, Herrera et al. 1998). The most well-known phenomenon is

masting : trees synchronously produce a large numbers of seeds with long time intervals (years) between these events, when few seeds are produced (Kelly 1994, Koenig and Knops 2000). There are several explanations for this phenomenon: the predator saturation hypothesis suggests masting events result in large number of seeds that satiate predators, in order to reduce seed loss to seed predators (Kelly 1994). The pollination efficiency hypothesis assumes wind pollinated species can achieve greater pollination efficiency through synchronized above-average flowering effort, leading to masting. This is most likely to happen to wind-pollinated tree species, since they do not risk saturating pollinators (Kelly et al. 2001). Kelly & Sork (2002) showed support for both the predator saturation hypothesis and the pollination efficiency hypothesis, as they found predator-dispersed species have higher variation in seed production than frugivore-dispersed species, and wind-pollinated species have higher variation than biotically pollinated species. Another explanation for masting is the resource matching hypothesis that posits that the variation of seed production is a response to available resources for seed production, including weather conditions, which are a sign of resource availability (Houle 1999, Kelly and Sork 2002). It is known that adverse weather, like drought or frost can sometimes prevent seed production (Sork et al. 1993, Houle 1999). But the previously mentioned studies support the explanation that masting is more likely to be an evolutionary adaptation.

There remains no consensus on the causes of masting in trees and how to predict its occurrence. Consequently, few attempts have been made to introduce it into forest models (Pearse et al. 2016, Vacchiano et al. 2018). Studies have also shown high variability in seed production among individuals in a population, suggesting that our understanding of the factors controlling fecundity is limited (Clark et al. 2004, Ibáñez et al. 2007). An important change in tree fecundity caused by ongoing climate change is increasing CO_2 concentration, as seeds are large carbon sinks and higher CO_2 concentrations are likely to change reproductive allocations within plants (Kirschbaum 2000, Jablonski et al. 2002). Various effects of CO_2 on plant fecundity has been found in plants (Jablonski et al. 2002), and an

experimental study also showed tree fecundity does increase with rising CO_2 concentration (Ladeau and Clark 2006).

Seed dispersal

The dispersal of trees has been of interest to researchers for a long time. Dispersal agents of plants can be wind, water and animal. Seeds can also be dispersed by ballistic dispersal or just drop with gravity. However seed dispersal is not always carried out by one agent, for example, seeds dispersed by wind can also be moved by animals after reaching ground (Nathan and Muller-Landau 2000). Trees have developed combinations of functional traits in adapting to different dispersal agents, known as dispersal syndromes (Clobert et al. 2012). Seeds dispersed by wind tend to be small and light, and often have wing or plume like structures; seeds dispersed by animals are usually contained in large, fleshy fruits, and have characteristic odours, colours, or nutrient contents associated with the specific animal dispersers; while water dispersed seeds are small and resistant to sinking (Howe and Smallwood 1982, Primack 1987).

Dispersal is a key process for tree population persistence and shaping the distribution of trees. Dispersal enables seeds to colonize new suitable habitat, such as recently created tree gaps, which are important for regeneration of trees in closed canopy forests. Another important advantage of dispersal is that seeds can escape potentially high density dependent mortality near adult trees, caused by associated predators and pathogens (Janzen 1970, Wang and Smith 2002). Many studies have confirmed the prevalence of density-or distance dependent mortality near adult trees, especially in tropical forests (Harms et al. 2000, Yamazaki et al. 2009, Metz et al. 2010). For animal dispersed species, a possible advantage is directed dispersal: dispersers can deposit seeds non-randomly into suitable sites and improve seedling establishment (Howe and Smallwood 1982). Evidence of directed dispersal has been found in bird-, rodent- and ant-dispersed plants, for example, the bellbird (*Procnias tricarunculata* Verreaux & Verreaux) increases the chance of dispersing seeds of a neotropical tree species (*Ocotea endresiana*) into canopy openings, than would be expected by chance (Wenny and

Levey 1998). In addition, rodents in the Sierra Nevada prefer to cache seeds at microsites favourable for seed survival (Briggs et al. 2009).

In practice the way to model seed dispersal often depends on the type of dispersal. Broadly, the modelling of seed dispersal patterns are carried out by either phenomenological models or mechanistic models (Levin and Muller-Landau 2003). Phenomenological models involve fitting a dispersal kernel from observed spatial distributions of dispersed seeds, usually collected via seed traps. A dispersal kernel is a probability density distribution of dispersal distance or location of seeds, usually a Gaussian distribution, the negative exponential, or the inverse power law distribution (Clobert et al. 2012). On most occasions, as identifying exact source of seed is difficult, the fecundity of possible source trees need to be estimated jointly with the dispersal kernel, and the tree locations need to be mapped. Collectively, this increases the amount of work needed to collect the necessary data, and complicates the accurate estimation of dispersal parameters (Levin and Muller-Landau 2003). The fecundity of trees is typically estimated by reference to the size of parent trees (e.g. the Diameter of the trunk at Breast Height (DBH) or its basal area). The first to apply all these data to estimate seedling dispersal kernels was Ribbens (1994), and various alternative dispersal kernels and improvements on existing ones have been proposed (Clark et al. 1999b, Katul et al. 2005, Klein et al. 2006, Nanos et al. 2010). In practice it is often used to fit seed distribution and seedling and sapling recruitment.

Mechanistic models seek to predict the location of dispersed seeds by understanding the characteristics of the dispersal processes. These models are usually more complex than the phenomenological models described above, and properly designed models can offer mechanistic explanations for dispersal patterns and predict dispersal independently of the observed seed distribution data (Nathan et al. 2003). Most mechanistic models are designed for wind or animal-dispersed seeds. Mechanistic wind dispersal models are based on physical theories relating to airborne particle dispersion, with varying levels of realism and complexity (Kuparinen 2006). Important factors determining dispersal distance of seeds by wind are seed

release height, terminal velocity of seeds, horizontal and vertical wind speed (Soons et al. 2004). The parametrization of mechanistic wind-dispersal models typical require detailed metrological data of studied area. Simpler mechanistic wind-dispersed models are usually deterministic, while complex ones try to incorporate stochastic fluctuation of wind speed at vertical and horizontal directions with various methods (Nathan et al. 2002, Kuparinen 2006).

Models for animal-dispersed seeds are less well developed compared to those for wind-dispersed seeds, as detailed data of animal behaviour, like foraging activity, subsequent movement and seed displacement, or tracking of tagged seeds is needed to fit these models. Mechanistic models of animal dispersal have been developed for several taxonomic groups including monkeys and birds (Russo et al. 2006, Merow et al. 2011). These models often combine simulations of animal movement and seeds retention in animal guts, both of which can be very variable (Levin and Muller-Landau 2003). The distribution and abundance of the food source, competition pressures and predation risk can all affect an animal's visit rate to a source plant, its foraging time and subsequent movement. An animal's size and gender can also affect fruit removal rate and gut retention time (Côrtes and Uriarte 2013). Deciding which factors are the most important for building an animal-dispersal model is challenging.

A relatively new and promising way of studying seed dispersal is to use genetic methods. When seeds and all possible source trees are genotyped, parental analysis can be used to assign each seed to its parent, providing accurate knowledge of dispersal distance. This method can help fitting both phenomenological and mechanistic models. Though expensive and requiring a large amount of data and analysis, there have been studies utilizing genetic methods to fit dispersal kernels and explore the relationships between seed, seedling and adult tree distributions (Robledo-Arnuncio and García 2007, Steinitz et al. 2011).

One important and challenging study subject in seed dispersal study is long distance dispersal, which is believed to be the key driver of rapid range expansion of plants (Nathan 2006). In 19th century the famous 'Reid's paradox' was proposed based on the disparity between current distribution of oak and distribution suggested by fossil record, as the observation of

oak dispersal rate wouldn't allow it to reoccupy its current distribution after ice age (Clark et al. 1998a). Many researchers suggest rare and non-standard ways of dispersal are involved to disperse seeds at long distance, like wind-dispersed seeds occasionally dispersed by birds over long distance (Higgins and Richardson 1999, Cain et al. 2000). Long distance dispersal events are rare but disproportionately important, influencing migration and invasion rates of tree species allowing trees to occupy remote habitats that they could not reach using standard dispersal (Higgins and Richardson 1999, Nathan et al. 2008). Long distance dispersal is considered to be key to rapid range expansion of trees during interglacial period and in a time of rapid climate change. It is expected that long-distance dispersal will be crucial for trees to catch up with changing climate and escape extinction, and will be important in predicting the expansion rate of invasive organisms (Loarie et al. 2009, Normand et al. 2011). As long-distance dispersal is mainly carried out via rare events, like storms, hurricanes or human transport, it is very difficult to observe and measure. So far, there isn't a satisfying way of quantifying long distance dispersal and incorporating it in models (Gillespie et al. 2012).

Seed Germination

Post-dispersal seed establishment processes consist of seed germination, growth and survival. Studies have shown that seed size has an important impact on germination success as larger seeds can germinate from deeper soils and have longer longevity, and seed size is related to the environment conditions needed to trigger germination, for example, germination of small-seeded tropical trees is promoted by light while large-seeded ones germinate equally in light and darkness (Pearson et al. 2002). Usually seeds require a combination of conditions to trigger germination and they may be dormant for years before requirements are met (Finch-Savage and Leubner-Metzger 2006). The triggering of germination is usually regulated by many environmental factors like light, temperature and moisture (Vdzquez-Yanes and Orozco-Segovia 1993), for example, most open-habitat species require adequate light to germinate (Pearson et al. 2002). Many temperate tree seeds need a period of chilling followed

by a warm period to break dormancy and in seasonal tropical forests germination often peaks after the rainfall season (Bazzaz 1979, Pearson et al. 2002, Doody and O'Reilly 2011).

The existence of a dormant seed bank can be important for persistence, for example, shade intolerant trees can rapidly colonize gaps created by disturbance via a pre-existing seed bank (Dalling et al. 1998, Tierney and Fahey 1998). Increases in both light and soil temperature could suggest formation of gaps and break dormancy of tree seeds (Finch-Savage and Leubner-Metzger 2006). Even though the abundance and longevity of woody plants seeds are generally low and short in temperate soil seed banks, they could still contribute a significant fraction to seedling recruitment (Hille Ris Lambers et al. 2005). The dormancy mechanism is considered an adaption to avoid unfavourable climate conditions (Nakashizuka 2001). The delay in germination could also be a way to avoid competition during masting or reduce sibling competition (Hyatt and Evans 1998).

Seedling growth and survival

Growth and survival processes are both affected by a series of abiotic and biotic factors. The requirement of different environment factors for seedling survival and growth is an important component of the regeneration niche of a tree species (Poorter 2007) , and partitioning of regeneration niches is believed to be critical for coexistence of different tree species (Denslow 1987, Valladares and Niinemets 2008).

Growth and survival of seedlings can be affected by abiotic factors like light, soil moisture, temperature and soil nutrients. The key factor affecting seedling performance in forest is usually considered to be light. The distribution of light can be highly heterogeneous in forests, largely due to the creation of gaps with the natural death of mature trees and other disturbance like fire, wind and human management (Canham et al. 1994, Yamamoto 2000). The heterogeneity of light distribution allows trees with different light requirement to coexist. Much research has been made on light's role on affecting seedling establishment and driving forest succession. One significant response of tree seedlings to light variation is a trade-off

between high light growth and low light survival, which has been found in various forest communities (Kobe et al. 1995, Walters and Reich 1996a, Lin et al. 2002, Kneeshaw et al. 2006, Coomes et al. 2009, Kunstler et al. 2009). This trade-off is believed to be important for the coexistence of shade tolerant and shade intolerant species and is thought to be a key driver of forest succession (Silvertown 2004, Valladares and Niinemets 2008). Differences in shade tolerance have been attributed to different carbon allocation strategies, where shade tolerant species put more resources in defence against herbivores and pathogens as well as into storage, enhancing their survival probability in shade, whereas shade intolerant species allocate more resources into growth (Bazzaz 1979). This is reflected in varying functional traits of seedlings with different light requirements. Shade intolerant seedlings tend to have lower root: shoot ratios, higher leaf mass per unit area and higher leaf area ratios than shade tolerant species (Walters and Reich 1996b, Wright et al. 2010).

The availability of soil nutrients like nitrogen and phosphorus are important resources affecting seedling growth and survival. The experimental addition of important nutrients like nitrogen and phosphorus often have a significant positive effect on growth of nutrient-limited seedlings (Ericsson and Ingestad 1988, Walters and Reich 2014). Studies on seedling survival and nutrient availability are relatively few and results are variable (Record et al. 2016). The differences in the utilization of soil nutrients among species can be an important component partitioning regeneration niches (Silvertown 2004). There are studies showing trade-offs between survival on fertile soil and growth rate on infertile soil (Schreeg et al. 2005, Russo et al. 2007), and these studies can be made alongside trade-offs between high light growth and low light survival. The effect of soil nutrients could also interact with the effect of light: the allocation between root and leaves of seedlings may differ at different light levels and affect the absorption capacity of soil nutrient and water (Coomes et al. 2007). Differences in growth rate response to nutrient supply of different tree seedlings are marked in both tropical and temperate tree species: the minimum light level for nutrient addition to have positive effect on growth rate varies a lot among species (Coomes and Grubb 1998).

Water availability is another factor key to seedling performance, especially in some forest ecosystems such as Mediterranean forest (Allen et al. 2010) while flooding and waterlogging can be restricting in other ecosystems like flood plains in Northern America (Greene et al. 1999). In many habitats, light intensity is negatively correlated to water availability (Monographs 2012). To improve water uptake, seedlings need more biomass allocated to roots and reduced foliage area to decrease evaporation, which in turn lowers light capture efficiency in shade (Lusk 2004). Niinements and Valladares (2006) have found in the northern hemisphere, that a general pattern of shade tolerance being negatively correlated with both drought tolerance and waterlogging tolerance.

The most prevalent and well-studied biotic effect on seedling growth and survival is the Janzen-Cornell effect, a density dependent effect that seedlings near conspecific trees suffer higher predation pressure, more attacks from pathogen and greater competition from siblings (Janzen 1970). This can be an important factor shaping forest species distribution and coexistence pattern, as abundant species can be restricted by negative density dependent effects and rare species have increased chances to survive. Many studies have provided support for this by showing negative density dependent effect on growth and survival of seedlings in both temperate and tropical forests (Clark and Clark 1984, Metz et al. 2010, Sheffer et al. 2013, Comita et al. 2014). In contrast, mechanisms may counter the negative effect of a conspecific adult: some studies have shown that seedlings near conspecific adults have higher probability of being infected with beneficial mycorrhizal fungi, which can improve their performance (Liang et al. 2015).

Apart from negative effects of adult trees, competition from other seedlings and understorey plants can also affect seedling's growth and survival. However, Moles and Westoby (2004) found that evidence in the literature that competition between established vegetation and seedlings caused seedling mortality was rare, and competition is probably not the main cause of seedling mortality. Identifying the cause of seedling mortality is difficult and the effect of competition can be under-reported. Understorey shrubs can have mixed effect on seedlings:

they can compete for light and nutrient with seedlings but can also act as barrier from herbivores or cast shade that reduces water evaporation. For example, brambles have been found to reduce predation of deer on tree seedlings (Harmer et al. 2010). Various results of shrubs on seedling performance have been found including inhibition, facilitation or no significant effects (Berkowitz et al. 1995, Harmer 2002, Beckage and Clark 2003) The effects of shrubs on seedling establishment are complex and can vary with micro stage conditions, species traits, and development stage of seedlings (Holl 2002).

Predicting forest dynamics with models

Knowledge about important forest processes has been widely used in computer models. Models which simulate changes in forest composition, abundance and distribution are valuable tools for testing effect of environment changes on forest. Succession of forest and composition changes usually take tens or hundreds of years and forest models are important tools to carry out experiments otherwise impossible in real life. Rapid climate changes also require realistic and accurate modelling methods to study responses of forests. The rising temperature has caused changes in the distributions of many plant communities, pushing the tree line to higher elevations and causing invasion of forests into grassland and tundra (Walther et al. 2002, Parmesan 2006a, Kelly and Goulden 2008). The increasing frequency of drought is also posing potential threat to recruitment of forest (Allen et al. 2010). Thus, forest models are particularly important for research and conservation of forest in face of global change.

There are various ways of modelling forests at different spatial and temporal scales, and the design and choice of models depend on the goals of the research. Species distribution models are widely used in predicting species distribution shifts with climate changes, by using statistical relationships fitted from observed climate conditions and occurrence or abundance of organism. Such models have been be used to project forest distribution in future climates (Thuiller et al. 2005, Dobrowski et al. 2011, Ruiz-Labourdette et al. 2012). However, most species distribution models lack explicit representation of ecological processes like dispersal

and establishment, and assume species distribution are in equilibrium with environment, which is not always the case (Thuiller et al. 2013, Snell et al. 2014).

Process-based models are another important way of modelling forest dynamic. By incorporating ecological processes, they provide a higher level of realism and better understanding of environment changes on communities and populations. Process-based models have huge variations in the level of detail that is modelled. A model can simulate growth, reproduction and mortality of individual trees or model underlying physiological processes like photosynthesis, uptake of nutrients and allocation of carbon (Reynolds et al. 2001). Generally, process-based models tend to have large number of parameters and require large amount of data to calibrate, which is a key limitation in their application (Snell et al. 2014).

Process-based models are also various in their spatial scale. The earliest process-based forest models focussed on modelling single or several forest stands, and they are often called gap models (Bugmann 2001). Some gap models can model individual tree dynamics in several patches (Botkin et al. 1972), while some models are spatially explicit and individual-based, tracking growth to death of single tree with explicit locations, as in the model SORTIE (Pacala et al. 1996). As environmental changes directly work on individuals, this high level of detail can help models make accurate predictions, but it also increases the amount of computation and limits the application of model predictions to larger spatial scales. With the development of landscape ecology, and the increase in requirements to incorporate disturbance, like fire, on larger spatial and temporal scale, forest landscape models were developed to model a region of hundreds or thousands of hectares (He 2008, Dai et al. 2015). These models usually use grid cells as basic spatially modelled unit. Individual trees in each cell are assigned to cohorts according to species, age or height for convenience of computation (Schumacher et al. 2004, Lischke et al. 2006). Dynamic global vegetation models (DGVM) are used to study distribution of vegetation, carbon cycle and effect of climate changed at continental or global scale. They can simulate biogeochemical cycles,

important ecological processes and are coupled to General Circulation Models to reflect climate change (Cramer et al. 2001). In these models, species with similar ecological characteristic are often grouped into the same plant functional types (PFTs) and share parameters. Treatment like this could ignore many important species level details, which may restrict ability of models to predict future forest dynamic (Quillet et al. 2010).

Early life stages of trees are represented differently among models. In forest gap models like FORMIND and SORTIE, onset and amount of seed production is described as a function of tree size and age (Pacala et al. 1996, Köhler and Huth 1998). While in DGVM like LPJ-GUESS, number of propagule production is a function of assimilated carbon allocated to reproduction (Sitch et al. 2003). In both cases seed production is not affected by environmental conditions directly. As changing climate conditions, like increasing CO_2 concentration can affect reproduction of trees, linking seed production directly to climate would be useful investigating forest response to climate change (Snell et al. 2014). Generally seed dispersal is either represented as perfect dispersal or by dispersal kernel. Perfect dispersal assumes seeds of all species can arrive at every simulated site with suitable condition for establishment, which is often not realistic. Most models use statistical dispersal kernels, but mechanistic dispersal models for wind have been widely used and mechanistic models for other vectors, like animals are also progressing (Bullock et al. 2017). Further incorporation of mechanistic dispersal models into forest models could lead to more accurate prediction of forest range changes. Seedling stages are often not explicitly included in many forest models, due to large number of seedlings, instead young trees above a threshold size are generated directly (Snell et al. 2014). In other models, seedling establishment can be related to factors like light, soil and landcover. As discussed in previous sections, seedlings establishment are sensitive to external factors like light, nutrient and herbivory. Ideal forest models should include these factors to model realistic seedling establishment.

In this thesis I used SORTIE for modelling. As a forest gap model, SORTIE is more suitable for studying forest dynamic at stand scale than forest landscape models like LANDIS.

Compared to gap models treating patches as basic spatial unit, like JABOWA family, SORTIE tracks individual tree spatial explicitly, which is more realistic (Bugmann 2001). SORTIE is also conceptually simple in that is considered that all trees are competing for only one resource – light (Evans et al. 2015). It has been extensively used in North America and New Zealand forests (Pacala et al. 1996, Kunstler et al. 2009, Ameztegui et al. 2010). SORTIE has been partially parameteized for Wytham Woods and used for studying effect of changin ggrowing season on tree population, which provides a good basis for this work (Carey 2015). Regeneration processes from seed production, seed dispersal to seedling establishment can also be explicitly modelled in SORTIE.

Objectives, material and structure of this thesis

Objectives

Knowledge of tree regeneration is very important for understanding forest dynamics and is necessary to make predictions with forest models. However, much basic data about regeneration stages, especially data about seed production and dispersal of deciduous trees in Europe and Britain, despite their importance, are still scarce. Even in a well-studied site like Wytham Woods, there is no long-term monitoring of seedling growth, survival and their response to environment conditions. Studying these would help us have better understanding of tree community dynamics and provide data necessary for model parameterization. There are two major objectives of this thesis: (1). Collection of data on seed production and dispersal, seedling survival and growth for common tree species and explore their relationship with environmental conditions. (2). Parametrizing a model with data collected in (1) and investigate the impact of regeneration processes on forest dynamics.

Study site and species

The field-work was carried out at Wytham Woods, Oxfordshire, U.K., which has been owned and managed by Oxford University since 1942. This is a 400 ha semi-natural ancient mixed woodland. It has been defined into five areas based on management histories: undisturbed

ancient semi-natural woodland; disturbed ancient semi-natural woodland; secondary woodland; 19th century plantation and 20th century plantation (Morecroft et al. 2008).

The studied species are ash (*Fraxinus excelsior* L.), sycamore (*Acer pseudoplatanus* L.), and beech (*Fagus sylvatica* L.). All these species are long-lived, frequently surviving up to around 500 years, with ash and sycamore having wind dispersed seeds, whilst beech is dispersed by animals (Table 1.1).They are all common components in temperate European forests. Ash is one of the most abundant tree species in Britain and provides valuable timber (Packham et al. 2012). It is also the second most abundant tree species at Wytham Woods (Kirby et al. 2014). Ash is a tree with strong colonization and competition capacity (Thomas 2016). The conservation of ash has received extra attention recently because of the arrival and spread of ash-dieback disease through Europe (Needham et al. 2016). Sycamore is native and widespread in Europe but may have been introduced to Britain by the Romans, about 2000 years ago. It has been viewed a threat to biodiversity in Britain, but also been found supporting a range of epiphytes, herbivores and ground flora (Morecroft et al. 2008, Hein et al. 2009). Sycamore often occur at the same sites as ash, and a study on their interactions showed cycles of regeneration between ash and sycamore (Waters and Savill 1992). In Wytham Woods, sycamore has become the most abundant tree species and its impact on conservation is worth detailed study. Beech is also one of the most widespread trees in Europe. Beech fruits are important food source for many animals and it has may important ecological functions (Packham et al. 2012). It has a well-known masting cycle of 2-3 years. In Wytham Woods, beech is not an abundant species and most trees exist as plantation trees.

In the seed dispersal chapter, I have also studied seed production and dispersal of birch (*Betula* L. spp.). Birch is a short-lived, wind-dispersed pioneer tree species and it is only found in small groups in Wytham Woods (Table 1.1). Its number is predicted to be decline in Wytham Woods (Carey 2015). Unfortunately, there were not enough data of seedling growth and survival of birch.

Table 1.1 Some ecological characteristics of the studied species.

Species	Shade tolerance	Drought tolerance	Dispersal agent	Longevity	Shade
Ash	2.66	2.5	Wind	100-500	deep
Beech	4.56	2.4	Animal	100-500	deep
Birch	1.94	1.56	Wind	10-100	light
Sycamore	4.2	2.73	Wind	100-500	deep

* Shade and drought tolerance are from Niinemets and Valladares (2006), ranking from 0 (no tolerance) to 5 (maximal tolerance).

Structure of thesis

For chapter 2, I collected seed dispersal data with seed traps, modelled seed production and the seed dispersal kernels of four common tree species using the inversing modelling approach. I explore the effects of tree density on seed production and dispersal.

In chapter 3, I estimate the response of diameter growth of seedlings to light intensity for three species and established an allometric relationship between seedling trunk diameter at 10 cm and height.

In chapter 4, I studied the response of seedling size survival probability to light intensity, seedling size and herbivory with mark-recapture methods.

In chapter 5, I incorporated the regeneration processes studied in previous chapters into a forest model, SORTIE, to make predictions of future dynamics in a stand with similar species composition of Wytham Woods. I compared the result with a model without seedling regeneration processes.

Chapter 6 is the final discussion

Chapter 2 Fecundity and seed dispersal of four common tree species at Wytham Woods, UK

Abstract

Seed production and dispersal are the starting points of forest regeneration. Both processes are affected by a series of environmental factors. Inverse modelling is a powerful approach to study seed dispersal, but applications on European tree species are relatively rare. In this chapter I used inverse modelling to estimate fecundity and seed dispersal kernels of four common tree species (three wind-dispersed species and one animal-dispersed species) at Wytham Woods, UK, as well as exploring effect of neighbouring tree density on tree fecundity and dispersal. The result shows the prediction of seed dispersal pattern prediction can be improved by incorporating neighbouring environmental conditions. However, both seed production and dispersal kernel showed high temporal variation.

Introduction

Seed production and dispersal are key starting points for the recruitment of trees. Seed dispersal is recognised to have profound implications on tree demography, forest structure, diversity and succession (Wang and Smith 2002). Dispersal from parents can also help seedlings escape the higher negative density dependent mortality arising from pathogens and herbivores near their parents (Janzen 1970). Negative density dependence survival of tree species has been found to be common in tropical and temperate forest communities and has profound effects on forest community composition (Harms et al. 2000, Metz et al. 2010, Johnson et al. 2012). Dispersal limitations can also be important in maintaining diversity. Lack of local seed sources or failure of dispersal could exclude a tree from suitable site. In tropical forests, gaps can be occupied by species that happen to be present when gaps were created instead of the most competitive species (Hubbell et al. 1999, Brokaw and Busing 2000). Over larger spatial scales, relatively rare long distance dispersal events have been

considered to be important for tree colonization across fragmented landscapes, and is likely to have been critical in, for example, the rapid colonization of trees in northern Europe after the most recent glacial period (Clark et al. 1998a, Cain et al. 2000).

In an age of rapid climate change, trees are being challenged to respond to changing climatic conditions. It is likely that this rapid climate change is a consequence of anthropogenic emissions of greenhouse gases, and the trend is predicted to accelerate in next century (IPCC 2013, 2014). Climate change is expected to drive species ranges towards higher latitudes and elevations, with expansion of the leading boundaries and contraction of the trailing boundaries of those ranges (Walther et al. 2002, Parmesan 2006a, Thomas 2010). Changes in species range has already been observed in many taxonomic groups including both plants and animals (Hickling et al. 2005, Lenoir et al. 2008, Thomas 2010, Chen et al. 2012). Rapid climate change poses challenges for species, as suitable climate conditions may disappear within the current range and similarly areas that were previously unsuitable may become part of the climatic niche (Loarie et al. 2009). To persist under changing climate, species need to track suitable climate spatially via dispersal.

Climate tracking via dispersal may be particularly difficult for trees, especially if they have limited dispersal ability relative to the rate of climate change. Predicted rates of climate change may require higher migration rates than historical records suggest has occurred in the past (Iverson et al. 2004). Even trees that had high migration rates during the Quaternary interglacial period, and recolonized new habitat rapidly, today also face anthropogenic influences on the landscape, which has led to habitat loss and fragmentation. Thus climate tracking processes may be much more difficult today than was apparent in the past (Thomas et al. 2004, Corlett and Westcott 2013). Climate change and human influences on the environment both present enormous challenges for biodiversity conservation, as protected areas may fail to be suitable for some species. Many studies have shown that plants, including trees, already have elevational range shifts towards higher altitude in response to climate change (Lenoir et al. 2008, Beckage et al. 2008, Kelly and Goulden 2008, Brusca et al. 2013),

but evidence of trees migrating to higher latitudes remains scant (Corlett and Westcott 2013). It is likely that elevational shifts require dispersal over shorter distances than latitudinal shifts. Potentially, dispersal limitations may result in a failure of trees to track climate over larger spatial scales, and assisted migration may prove to be necessary to prevent extinction (Araújo et al. 2011, Schwartz et al. 2012).

Given the importance of the dispersal process, models that predict the effect of climate change on plant distribution should consider dispersal (Thuiller et al. 2008). However, of the numerous studies that have been conducted to predict the potential future distribution of trees under climate change, most have employed correlative models to find relationships between species presence and environmental conditions, with predictions usually being made at global or continent scales (Dawson et al. 2011, Pagel and Schurr 2012). Failure to consider the dispersal process increases uncertainty in predictions and limits their application to biodiversity conservation. Most correlative models also lack other important biological processes and interactions between species, so it is widely acknowledged that correlative models should be interpreted with care (Araújo and Guisan 2006, Elith and Leathwick 2009). A useful alternative is provided by process-based modelling which include important biological processes like growth, mortality, and dispersal. Many process-based forest growth models have been developed and used to model succession, disturbance and impact of environmental change (Hartig et al. 2012). They can provide reliable predictions, informed by biological knowledge of vital processes. This chapter is part of a project to introduce dispersal parameters of individual species into SORTIE, an individual tree-based model that estimates forest dynamics in British forests. It will provide support for any similar ecological models that require an understanding of the dispersal process.

The dispersal of trees has been subject of intensive studies. Three general approaches have been used for quantifying dispersal patterns of tree seeds/seedlings (Canham et al. 2006) : (1) Direct measurement from various locations around a single, isolated individual (Stoyan and Wagner 2001). But it is important to recognise that seed production and dispersal of an

isolated tree can be very different from one in a dense environment. (2) Mechanistic models associated with the dispersal vector of seeds. Aerodynamic models have been used to study the dispersal of wind-dispersed seeds (Greene and Johnson 1989, Katul et al. 2005) and models incorporating animal behaviour have been used for animal-dispersed seeds (Russo et al. 2006). (3) Inverse modelling (IM) which utilizes the observed spatial distribution of seeds or seedlings plus the size of potential source trees has also been used estimate dispersal parameters (Ribbens et al. 1994, LePage et al. 2000, Clark et al. 2005, Martínez and González-Taboada 2009).

Predicting dispersal of trees over large scales (>1km) remains difficult as data of long distance dispersal is hard to collect and quantify (Higgins et al. 2003, Hampe 2011). In this chapter I use IM, a well-established method that has been adopted by many similar studies to study seed dispersal of four tree species (Clark et al. 1998b, 2005, Astrup et al. 2008, Martínez and González-Taboada 2009, Jang et al. 2013). The data required can be readily acquired by collecting dispersed seeds with seed traps. Relatively recent developments also allow the incorporation of environmental effects into inverse modelling, and that is thought to greatly improve the model's ability to predict and explain seed dispersal patterns (Schurr et al. 2008, Herrera et al. 2011).

Here, I estimated fecundity and dispersal kernels of four common canopy tree species in Wytham Wood (Oxfordshire, UK) and explored the effects of conspecific and heterospecific tree densities on these kernels. My hypothesis is that tree density has important effects on tree fecundity and dispersal. High tree density around a mother tree would decrease its fecundity via competition. In addition, it is likely that the effects of conspecifics may be more profound than that of heterospecifics, because individual trees of a species occupy the same niche. As far as dispersal is concerned, for wind dispersed trees, trees around a source tree and on the potential dispersal path may intercept seeds and reduce dispersal distances.

Method

Study site

Field work was carried out in Wytham Woods, Oxford (51° 46 ′ N, 1° 20 ′ W). It covers 400 ha and has been a research site of Oxford University since the 1940s. The woodland compromises ancient semi-natural woodland, naturally generated secondary woodland and plantations (Mihok et al. 2009). The mean annual temperature is 10ºC and the mean annual rainfall is 726 mm (Butt et al. 2009).

Collection of seed and measurement of trees

We placed 54 seed traps in six plots in Wytham Woods, with nine traps in each plot, following Clark et al (1998). The traps in a plot were arranged in two crossing transects. The traps were spaced at 10m intervals. The central trap was placed at the centre of a plot. Each seed trap consists of a mesh screen with area of 0.25 m^2 supported by PVC frame.

Fig. 2.1 Design of seed trap

Each plot was 70 x 70 m in size. Ash, sycamore and oak (*Quercus robur* L.) are most common canopy tree species. birch is also locally abundant in two plots. The main under canopy tree species are hawthorn (*Crataegus monogyna* Jacq.) and hazel (*Corylus avellane* L.). Two plots were in semi-natural ancient woodland and three plots were in secondary woodland. One plot was in a plantation of beech (*Fagus sylvatica*) and sweet chestnut

(*Castanea sativa* Mill.). The contents of each seed trap were cleared, and the collected seeds were counted every one or two weeks from September to February in 2015 and 2016. All trees with diameter at breast height (DBH) >15cm were mapped with a laser rangefinder (Hilti PD 40, UK) and a compass. Their DBH were also measured. These were considered to be possible source trees.

Fig 2.2 Locations of plots in Wytham Woods

Estimation of Fecundity and Dispersal Kernel

I used inverse modelling (IM) approach to model seed production and dispersal. This model estimates fecundity and dispersal using the observed spatial distribution of possible parent plants and seeds, finding the parameters that are the most likely to produce the observed spatial distribution pattern (Ribbens et al. 1994, Clark et al. 1999b).

The seed shadow of a single plant is the product of a fecundity function *Q* and a dispersal kernel *f*

Q is a function of plant size. We used basal area as our measure of tree size following Clark et al. (1999). Therefore:

$Q(G)=bG$ **equation 2.1** Schurr et al. (2008)

Where *G* is basal area and *b* is the fecundity parameter. *Q(G)* calculates number of seeds produced by a tree with basal area *G*.

The dispersal kernel *f* is a probability density function that describes the probability of seeds dispersing different distances from a parent tree (Nathan 2006). It is a function of dispersal distance *r* with a scale parameter *u* (mean dispersal distance in Lognormal kernel) and a shape parameter *p*:

$P=f(r,u,p)$ **equation 2.2** Schurr et al. (2008)

I compared performance of two commonly used dispersal kernels, 2Dt kernel and lognormal kernel on four species in each year and chose the best one based on AIC values for environmental effects analyses. The two kernels are based on mixture of Gaussian and Lognormal distribution respectively. The 2Dt kernel is a mathematical model, which is claimed to be suitable for fitting both local and long distance dispersal (Clark et al. 1999b). The lognormal kernel is based on micrometeorological model of seed dispersal by wind (Stoyan and Wagner 2001). They have been proved of good performance in previous seed dispersal studies and recommended by Clobert et al. (2012).

The 2Dt Kernel (Clark et al. 1999b) :

$$f(r) = \frac{p}{\pi u\left(1+\frac{r^2}{u}\right)^{p+1}}$$ **equation 2.3**

The Lognormal Kernel (Stoyan and Wagner 2001):

$$f(r) = exp\left[-\frac{\left(ln\, r - ln\, u - {}^{p}/_{2}{}^{2}\right)^{2}}{2p^2}\right] \Big/ (2\pi)^{3}/_{2} p r^2$$ **equation 2.4**

Therefore, the number of seeds received by a seed trap *i* with area *A* is the sum of seeds dispersed to it from all *T* possible parent trees.

$S_i=\sum_{j=1}^{T} Q(G) f(r)\, A$ **equation 2.5**

The number of seeds in one seed trap is assumed to follow a Poisson distribution. Therefore, the fecundity and dispersal parameters can be estimated using Maximum Likelihood method.

Incorporation of environmental effects

I followed Schuur et al. (2008) to model the environmental effects on a tree's fecundity and the dispersal of its seeds. I used tree density as the environmental variable (Schuur et al. 2008) as it can reflect intensity of competition and resistance to seed dispersal. A grid with 10x10m cells was superimposed on the study plots and the number of trees counted in each cell. To explore if there was an effect of species; conspecific and non-conspecific tree density were calculated separately for each species and both were used as environmental variables. Huge annual variation in seed production was observed. Also, the temporal variation of climate conditions like rainfall and wind speed may have an impact on both seed production and dispersal. Therefore, I added a year effect as a proxy for the unaccounted variations in environmental conditions between years. For data collected in 2015 the of value of year is marked as 0, and in 2016 it is 1.

To incorporate environmental effects into the standard IM, fecundity and dispersal parameters were firstly modelled as functions of the environmental conditions surrounding a tree. This models the environmental effects around the seed source.

For example, fecundity parameter b of tree i was modelled as:

$$b_i = exp(b_0 + b_{conspecific}E_{conspecific} + b_{heterospecific}E_{heterospecific} + b_{year}E_{year})$$ **equation 2.6**

Where $E_{conspecific}$ and $E_{heterospecific}$ are conspecific and heterospecific tree density of tree *i* in its cell. E_{year} is the year effect. b_0, $b_{conspecific}$, $b_{heterospecific}$ and b_{year} are 'intercept' and 'slopes' respectively. When values of slopes are zero, the model is equivalent to a standard model without environment effects. This approach also applies to dispersal parameter *u* and *p*:

$$u_i = exp(u_0 + u_{conspecific}E_{conspecific} + u_{heterospecific}E_{heterospecific} + u_{year}E_{year})$$ **equation 2.7**

$$p_i = exp(p_0 + p_{conspecific}E_{conspecific} + p_{heterospecific}E_{heterospecific} + u_{year}E_{year})$$ **equation 2.8**

Secondly the effect of environment conditions on a potential seed dispersal path was modelled. The absolute distance between a seed trap and seed source was transformed into an effective distance dependent on the environmental conditions on the dispersal path. Under this approach, locations with high resistance have large effective distances and decreased probability of seeds moving along it (Herrera et al. 2011). The effective distance is defined as:

$r' = \sum_c d_c * w_c$ **equation 2.9**

Where:

r' is the effective distance between the seed trap and a source tree.

c denotes all cells intersected by a straight line between the source and the cell

d_c is the length of the straight line segment in each cell.

w_c is the environmental resistance in cell c.

The environmental resistance w_c is modelled as:

$w_{c=}exp(\beta_w E_c)$ **equation 2.10**

where *Ec* is the number of trees in each cell as E in above.

With effective distance changed, the effective area of seed traps also needs to be modified, as traps in high resistance cell surrounded low resistance cell could have higher probability of receiving seeds:

$A' = A\frac{r}{r'}\exp(\beta_w E)$ **equation 2.11**

Where:

A' is the effective area and A is the actual area of the trap.

r is the actual distance from source to cell and r' is the effective distance calculated by equation 2.6.

E is the environmental variable in the cell where the seed trap was located.

Table 2.1 Symbols used in this chapter and throughout the thesis

Symbol	Meaning
b (equation 2.1,2.6)	fecundity parameter controlling number of seeds produced by a tree
u (equation 2.2, 2.7)	scale parameter of dispersal kernel
p (equation 2.2, 2.8)	shape parameter of dispersal kernel
w (equation 2.9, 2.10)	environmental resistance
a (equation 3.2)	asymptote of logistic function
b (equation 3.2)	the x value at the inflection point of the logistic growth curve
c (equation 3.2)	scale parameter of logistic growth function
S_i (equation 4.1)	survival probability of a seedling at sample occasion i
p_i (equation 4.1)	relocation probability of a seedling at sample occasion i
$\psi^{rs}{}_i$ (equation 4.1)	the probability of a seedling under state r at sample occasion i is in state s at sample occasion i+1, given it is alive at i+1

Modelling and Model Averaging

For three wind-dispersed species with two years of data, I modelled the effects of tree density and year on the fecundity and dispersal kernels, plus a path effect. Effect of tree density on fecundity consisted of conspecific and heterospecific tree density to reflect potential species-specific effect. Dispersal is modelled by tree density regardless of species as species composition is unlikely to affect interception of seeds. The path effect is also modelled with density of all trees for same reason.

For beech, for which there was only one year of data and which is mainly dispersed via barochory (dispersed via gravity) and animals, I include conspecific and heterospecific density on fecundity, and used only conspecific density as environmental variable affecting dispersal, as it has been reported that increased fruit abundance in the neighbouring environment has negative relationship on dispersal in other animal dispersed species (Herrera et al. 2011).

Alternative models were fitted for different potential combinations of effect types and environmental variables. For comparison I also modelled a 'standard model' without any environmental effects. This resulted in there being 19 models for ash, sycamore and birch and 12 models for beech. Because over dispersion existed in data, I used QAIC value instead of AIC value to compare performance of models. A lower QIAC value indicates better model

performance. Model with lowest QAIC is the best model. Models with difference in QAIC between the best model (ΔQAIC) <2 are considered equally good in performance. ΔQAIC within 4-7 means considerably less support for the models and difference greater than 10 means essentially no support (Burnham and Anderson 2002). I first estimated a variance inflation factor (v) and used the variance inflation factor to calculate QAIC (Burnham and Anderson 2002).

$v = \frac{2}{df}(lnL_G - lnL_S)$ **equation 2.12**

Where L_S is a saturated model with as many parameters as data points. L_G is the likelihood of the most complex model in study. df is the additional number of parameters to specify the saturated model (Richards 2007).

The QAIC value is calculated with v as:

$QAIC = -\frac{2}{v} lnL + 2K$ **equation 2.13**

where L is likelihood of model concerned and K is number of parameters.

To evaluate goodness of fit, I conducted linear regression between observed and predicted number of seeds. All analyses were done in R (R Core Team 2015).

There are chances of seeds coming from trees outside the plots. In this case the outer traps are the most likely to be affected. To test if there is a significant effect of seed immigration, I re-fitted all models excluding the outermost traps and compared parameters to the models obtained using all traps using Wilcoxon signed-rank test.

To deal with model uncertainty in parameter estimation, I used the model averaging approach on fitted models (Burnham and Anderson 2002) . First, a model weight **w** is calculated for each model according to their delta QAIC value:

$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_r^R -\frac{1}{2}w_r}$ **equation 2.14**

Where Δ_i is the ΔQAIC value of model i

Then I chose a set of models with cumulative w >95% as confidence set (Burnham and Anderson 2002). The model averaged parameter is calculated based on models in confidence set:

$$\bar{\beta} = \frac{\sum_{i=1}^{R} \beta_i}{\sum_{i=1}^{R} w_i}$$ **equation 2.15**

Where $\bar{\beta}$ is the model averaged parameter estimate and β_i is the estimate of model i. The average is only calculated over models where the variate of interest appears (Symonds and Moussalli 2011).

The unconditional standard error of model averaged parameters was calculated as:

$$SE(\bar{\beta}) = \sum w_i \sqrt{var(\beta_i) + (\beta_i - \bar{\beta})^2}$$ **equation 2.16**

Where $var(\beta_i)$ is the variance of parameter β in model i.

Parameter values, standard error and 95% confidence interval of model averaged parameters were calculated. I judged the model averaged parameter significantly different from zero if its 95% confidence interval did not contain zero.

Results

Species composition

Ash and sycamore are the two most dominant tree species, making up 28.7% and 24.7% respectively of the total of 1166 trees mapped. Other species were beech (15%), hazel (11.4%), oak (5%), hawthorn (4.8%), birch (3.6%) and others (4.7%). The species composition over the study plots reflect well tree abundance across Wytham Woods (Table 2.2). Averaged tree density across the 10x10 m cells varied from 0.19 trees/m^2 to 0.48 trees/m^2 between the six study plots, with an average 0.31 trees/m^2 for all plots.

Table 2.2 Species composition of trees mapped in study plots

Species	Total number of trees within survey plots	Percentage in mapped trees within survey plots	Percentage across the whole wood*
Ash	335	24.80%	23.2%
Beech	182	15.60%	10.4%
Birch	42	3.60%	9%
Hazel	135	11.57%	10%
Hawthorn	58	4.97%	8.6%
Oak	58	4.97%	9.5%
Sycamore	288	24.68%	22.7%

* Calculated from Evans and Moustakas (2016), in which numbers of each species surveyed in the Environmental Change Network plot at Wytham Woods were presented.

Seed collection

Ash, sycamore and birch accounted for most of the captured seeds. Animal dispersed seeds, from species such as hazel, and oak seeds were rarely encountered (<10 seeds/year) or were highly restricted in their occurrence, such as hawthorn (found in only one trap).

There was large annual variation in number of seeds collected (Fig 2.3). 2016 saw many more sycamore seeds than 2015. No beech seeds were collected in 2015 while there were 128 in 2016. As beech is known for having 2-3-year cycle of masting, our sampling period may have fallen across poor fruiting years. Paired t-tests showed collected ash seeds were significantly lower in 2016 while sycamore and birch had significant increases in seed numbers in 2016.

In total four species (ash, beech, birch and sycamore) have sufficient data to be modelled.

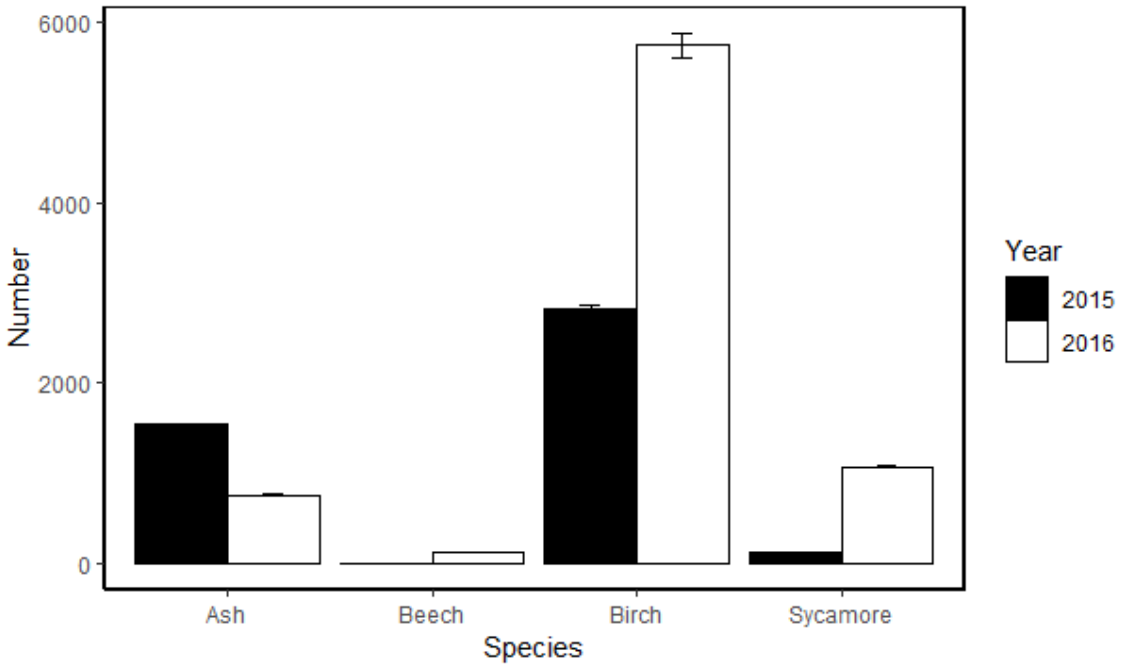

Fig.2.3 Comparison of number of seeds collected in 2015 and 2016 Bars represent standard error.

Effect of Tree Density on Fecundity and the Dispersal Kernel

It appears that the lognormal kernel (Stoyan and Wagner 2001) performed best in IM in all cases (Table 2.3), consequently it was chosen to analyse environmental effects.

Wilcoxon signed-rank test was used to compare the fecundity and dispersal kernels estimated from all traps on the plot (nine traps per plot) with those when the outer traps were excluded from the analysis. There was no significant difference ($p>0.05$), therefore there is no evidence of the results being biased by seeds from outside the plots.

Models with an environmental variable (incorporating tree density) performed better than the standard model in most cases (Table 2.4). Species have different model ranking (Table 2.4) and model averaged parameters (Table 2.5). No individual model has model weight $w>0.5$, reflecting high model selection uncertainty. Parameters of individual models are presented in Table 2.6 and 2.7

Table 2.3 Comparison of standard dispersal kernel performance for different species between two dispersal kernels

Kernel	Species	AIC
2Dt	Ash	1432.5
Lognormal	Ash	1388.3
2Dt	Beech	129.11
Lognormal	Beech	114.35
2Dt	Sycamore	2162.47
Lognormal	Sycamore	2146.2
2Dt	Birch	458.33
Lognormal	Birch	418.38

Table 2.4 Summary of model performance for all species ΔQAIC values are listed in descending order of size. Effects that might influence fecundity and dispersal (i.e. tree densities) that were considered in the model are shown (/ :no effect considered).

Species	Fecundity	Dispersal	Path Effect	ΔQAIC	w	R^2
Ash	Year	Year	Yes	0	0.26	0.52
Ash	Year	Year	No	1.39	0.13	0.51
Ash	Tree	Year	Yes	1.42	0.13	0.53
Ash	Tree	Tree+Year	Yes	1.57	0.12	0.45
Ash	Tree+Year	Tree	Yes	1.74	0.11	0.52
Ash	Year	Tree	Yes	1.91	0.10	0.49
Ash	Tree+Year	Year	Yes	2.85	0.06	0.53
Ash	Year	Tree	No	4.16	0.03	0.5
Ash	Tree	Year	No	6.06	0.01	0.55
Ash	Tree+Year	Tree	No	6.2	0.01	0.58
Ash	Tree+Year	Year	No	6.2	0.01	0.51
Ash	Tree+Year	Tree+Year	No	6.3	0.01	0.56
Ash	Tree	Tree+Year	No	6.79	<0.01	0.54
Ash	/	/	No	7.61	<0.01	0.41
Ash	Tree+Year	Tree+Year	Yes	8.14	<0.01	0.58

Table 2.4 continued

Ash	Year	Tree+Year	Yes	9.94	<0.01	0.52
Ash	Tree	Tree	Yes	13.6	<0.01	0.43
Ash	Year	Tree+Year	No	13.81	<0.01	0.53
Ash	Tree	Tree	No	20.33	<0.01	0.41
Sycamore	Tree+Year	Tree+Year	No	0	0.51	0.91
Sycamore	Tree	Tree+Year	No	1.39	0.25	0.85
Sycamore	Tree	Tree+Year	Yes	3.51	0.09	0.87
Sycamore	Tree+Year	Year	Yes	3.62	0.08	0.86
Sycamore	Tree	Year	No	3.99	0.07	0.9
Sycamore	Tree+Year	Year	No	11.39	<0.01	0.87
Sycamore	Tree+Year	Tree+Year	Yes	12.7	<0.01	0.89
Sycamore	Tree+Year	Tree	No	17.99	<0.01	0.87
Sycamore	Tree+Year	Tree	Yes	19.99	<0.01	0.87
Sycamore	Year	Tree	No	23.59	<0.01	0.85
Sycamore	Year	Tree	Yes	26.07	<0.01	0.84
Sycamore	Year	Tree+Year	No	27.31	<0.01	0.85
Sycamore	Year	Tree+Year	Yes	28.35	<0.01	0.84
Sycamore	Tree	Year	Yes	31.6	<0.01	0.85
Sycamore	Year	Year	No	34.44	<0.01	0.69
Sycamore	Year	Year	Yes	40.69	<0.01	0.72
Sycamore	Tree	Tree	No	117.2	<0.01	0.35
Sycamore	Tree	Tree	Yes	123.19	<0.01	0.34
Sycamore	/	/	No	149.31	<0.01	0.37
Birch	Year	Tree	No	0	0.38	0.81
Birch	Tree	Tree	No	1.46	0.19	0.74
Birch	Tree+Year	Tree	No	1.72	0.16	0.74
Birch	Year	Tree	Yes	1.86	0.15	0.81
Birch	Tree	Tree+Year	No	5.02	0.03	0.74
Birch	Tree+Year	Tree+Year	No	5.56	0.02	0.73
Birch	Tree+Year	Tree	Yes	5.99	0.02	0.77
Birch	/	/	No	7.16	0.01	0.62
Birch	Tree	Year	No	7.61	<0.01	0.72
Birch	Year	Year	No	7.83	<0.01	0.68
Birch	Tree+Year	Year	No	9.01	<0.01	0.72
Birch	Tree	Tree	Yes	9.1	<0.01	0.72
Birch	Year	Tree+Year	No	9.82	<0.01	0.72
Birch	Tree+Year	Tree+Year	Yes	10.98	<0.01	0.77
Birch	Tree	Tree+Year	Yes	11.5	<0.01	0.8
Birch	Tree	Year	Yes	12.94	<0.01	0.75
Birch	Year	Year	Yes	13.65	<0.01	0.71
Birch	Tree+Year	Year	Yes	16.37	<0.01	0.72
Birch	Year	Tree+Year	Yes	16.37	<0.01	
Beech	Heterospecific Density	Conspecific Density		0	0.36	0.86

Table 2.4 continued

Beech	Heterospecific Density	Conspecific Density	Yes	1.2	0.20	0.9
Beech	Conspecific +Heterospecific Density	Conspecific Density	No	1.36	0.18	0.91
Beech	Conspecific +Heterospecific Density	Conspecific Density	No	2.67	0.10	0.9
Beech	Conspecific Density	/	Yes	3.22	0.07	0.78
Beech	Conspecific Density	/	No	4.6	0.04	0.75
Beech	Heterospecific Density	/	No	4.94	0.03	0.63
Beech	Heterospecific Density	/	Yes	6.51	0.01	0.62
Beech	Conspecific Density	Conspecific Density	No	8.26	<0.01	0.53
Beech	/	/	No	10.18	<0.01	0.1
Beech	Conspecific Density	Conspecific Density	Yes	14.26	<0.01	0.68
Beech	Conspecific +Heterospecific Density	/	No	15.47	<0.01	0.38
Beech	Conspecific +Heterospecific Density	/	Yes	17.62	<0.01	0.38

Table 2.5 The model averaged parameters of all species Those parameters in which the range +95%CI to - 95%CI did not include zero are marked in bold.

Species	Param	Value	SE	95%CI
Ash	$b_{intercept}$	13.56	0.42	**(12.74,14.38)**
Ash	$b_{conspecific}$	-0.02	0.37	(-0.75,0.71)
Ash	$b_{heterospecific}$	-0.1	0.37	(-0.83,0.63)
Ash	b_{year}	-1.09	0.48	**(-2.03,-0.15)**
Ash	$u_{intercept}$	4.38	0.45	**(3.5,5.26)**
Ash	u_{tree}	-0.03	0.69	(-1.38,1.32)
Ash	u_{year}	-0.35	0.47	(-1.27,0.57)
Ash	$p_{intercept}$	-0.67	0.4	(-1.45,0.11)
Ash	p_{tree}	-0.18	0.44	(-1.04,0.68)
Ash	p_{year}	-0.75	0.37	(-1.48,0.02)
Ash	w	0.04	0.63	(-1.19,1.27)
Sycamore	$b_{intercept}$	11.29	1.36	**(8.62,13.96)**
Sycamore	$b_{conspecific}$	0.55	0.39	(-0.21,1.31)
Sycamore	$b_{heterospecific}$	-0.87	0.41	**(-1.71,-0.03**)
Sycamore	b_{year}	2.34	0.31	**(1.73,2.95)**
Sycamore	$u_{intercept}$	4.09	0.87	**(2.38,5.8)**
Sycamore	u_{tree}	-0.01	0.37	(-0.73,0.71)
Sycamore	u_{year}	-0.94	0.37	**(-1.67,-0.21)**
Sycamore	$p_{intercept}$	-1.27	1.36	(-3.94,1.4)
Sycamore	p_{tree}	0.07	0.44	(-0.79,0.93)
Sycamore	p_{year}	1.12	1	(-0.84,3.08)
Sycamore	w	0	0.34	(-0.67,0.67)
Birch	$b_{intercept}$	15.31	0.4	**(14.53,16.09)**
Birch	$b_{conspecific}$	0.23	0.48	(-0.71,1.17)
Birch	$b_{heterospecific}$	-0.2	0.49	(-1.16,0.76)
Birch	b_{year}	0.15	0.31	(-0.46,0.76)
Birch	$u_{intercept}$	4.58	0.34	(3.91,5.25)
Birch	u_{tree}	-0.23	0.11	**(-0.45,-0.01)**
Birch	u_{year}	0.17	0.3	(-0.42,0.76)
Birch	$p_{intercept}$	-0.09	0.28	(-0.64,0.46)
Birch	p_{tree}	-0.33	0.21	(-0.74,0.08)
Birch	p_{year}	0.07	0.35	(-0.62,0.76)
Birch	w	0.08	0.47	(-0.84,1)
Beech	$b_{intercept}$	10.23	0.86	**(8.54,11.92)**
Beech	$b_{conspecific}$	0.19	0.73	(-1.24,1.62)
Beech	$b_{heterospecific}$	0.36	0.37	(-0.37,1.09)
Beech	$u_{intercept}$	4.46	0.69	**(3.11,5.81)**
Beech	u_{tree}	-0.29	0.14	**(-0.56,-0.03)**

Beech	$p_{intercept}$	-0.56	0.27	**(-1.09,-0.03)**
Beech	p_{tree}	-0.26	0.13	**(-0.51,-0.01)**
Beech	w	0.06	0.78	(-1.47,1.59)

Ash

The only significant environmental factor in model averaged result is effect of year on fecundity. The model indicated that in 2016 fecundity of ash was ~8% lower compared to 2015. This is also observed in seeds collected (Fig 2.3). The expected effect of tree density on ash dispersal was not evident.

Sycamore

Effect of heterospecific tree density had significant negative effect on sycamore fecundity. In contrast to ash, sycamore fecundity increased in year 2016. Like ash, there is no significant effect of tree density on sycamore dispersal. However, estimated mean dispersal distance of sycamore decreased significantly from 59m in 2015 to 25m in 2016.

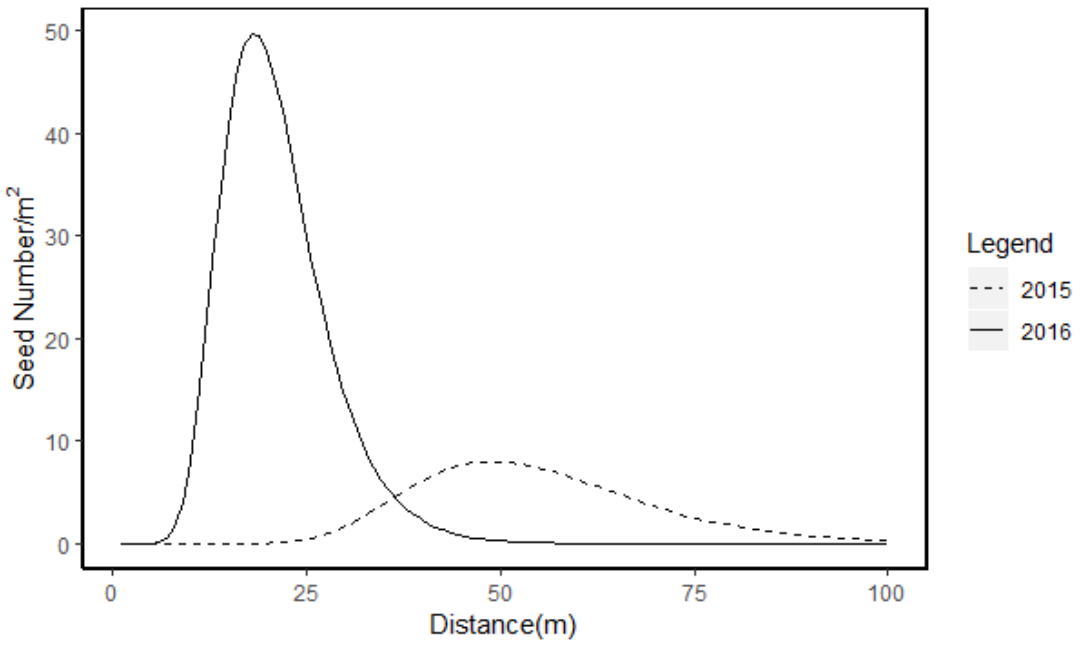

Fig.2.4 Comparison of Dispersal kernels of a sycamore tree producing 10,000 seeds in 2015 and 2016 based on model averaged parameters

Birch

Birch dispersal was significantly affected by tree density. The negative u_{tree} decreases mean dispersal distance of birch seeds (Table 2.5). Higher tree density around a birch tree decreased the mean dispersal distance of birch seeds. The dispersal curve is also more peaked in dense environments (Fig 2.5). However, the effect of tree density on dispersal path was not significant.

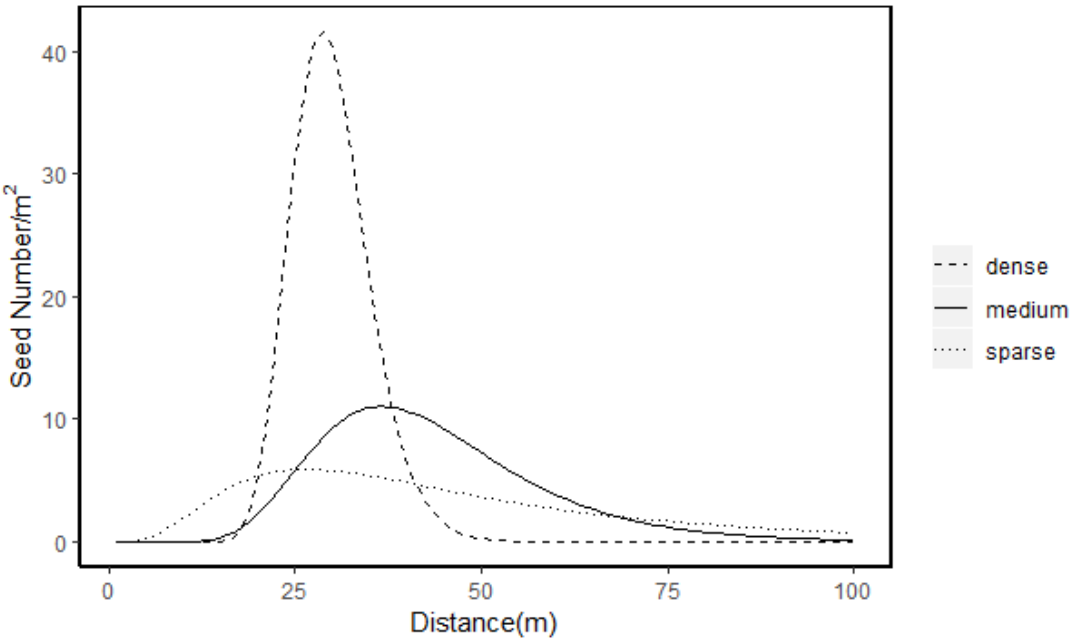

Fig.2.5 Dispersal kernels of a birch tree producing 10,000 seeds based on model averaged parameters

The different curves denote dense (0.5 trees/m^2), medium (0.3 trees/m^2) and sparse (0.1 trees/m^2) neighbouring environment.

Beech

Conspecific tree density has significant effect on beech dispersal (Table 2.5). Beech in environment with high conspecific density tend to have shorter dispersal distance and more peaked dispersal curve (Fig 2.6).

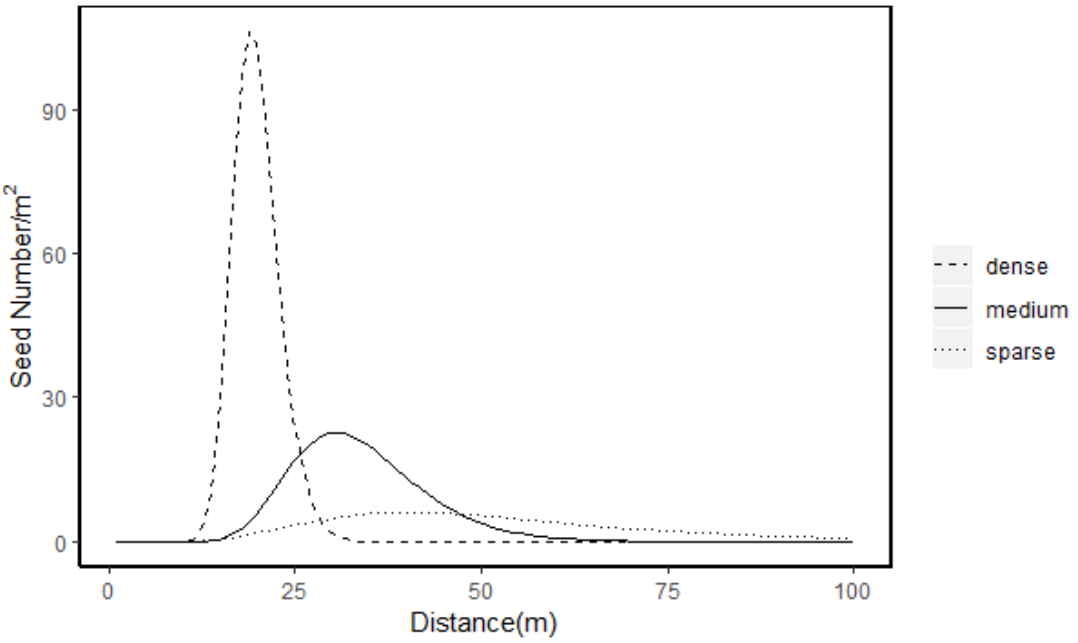

Fig.2.6 Dispersal kernels of a beech tree producing 10,000 seeds based on model averaged parameters

The different curves denote dense (0.5 conspecific trees/m^2), medium (0.3 conspecific trees/m^2) and sparse (0.1 conspecific trees/m^2) neighbouring environment.

Table 2.6 Parameters of individual models of ash, sycamore and birch Parameters with 95% CI didn't include zero were marked in bold.

Parameter	Fecundity	Dispersal	Path Effect	Species	Value	95% CI
$b_{intercept}$	Year	Year	Yes	Ash	13.42	**(13.85,14.98)**
$b_{intercept}$	Year	Year	No	Ash	13.52	**(12.96,14.1)**
$b_{intercept}$	Tree	Year	Yes	Ash	14.1	**(13.44,14.59)**
$b_{intercept}$	Tree	Tree+Year	Yes	Ash	13.44	**(12.87,14.1)**
$b_{intercept}$	Tree+Year	Tree	Yes	Ash	13.54	**(12.97,14.11)**
$b_{intercept}$	Year	Tree	Yes	Ash	13.2	**(12.44,13.58)**

$b_{intercept}$	Tree+Year	Year	Yes	Ash	13.9	**(13.35,14.49)**
$b_{intercept}$	Year	Tree	No	Ash	15.8	**(14.51,15.65)**
$b_{intercept}$	Tree	Year	No	Ash	12.67	**(12.1,13.24)**
$b_{intercept}$	Tree+Year	Tree	No	Ash	13.38	**(12.81,13.95)**
$b_{intercept}$	Tree+Year	Year	No	Ash	12.95	**(12.38,13.52)**
$b_{intercept}$	Tree+Year	Tree+Year	No	Ash	12.85	**(12.28,13.42)**
$b_{intercept}$	Tree	Tree+Year	No	Ash	12.63	**(12.6,13.2)**
$b_{intercept}$	/	/	No	Ash	12.8	**(12.51,13.65)**
$b_{intercept}$	Tree+Year	Tree+Year	Yes	Ash	11.6	**(1.49,11.63)**
$b_{intercept}$	Year	Tree+Year	Yes	Ash	11.91	**(11.34,12.48)**
$b_{intercept}$	Tree	Tree	Yes	Ash	13.98	**(13.41,14.54)**
$b_{intercept}$	Year	Tree+Year	No	Ash	11.75	**(11.18,12.32)**
$b_{intercept}$	Tree	Tree	No	Ash	15.49	**(14.92,16.5)**
$b_{conspecific}$	Tree	Year	Yes	Ash	-0.2	(-.73,.73)
$b_{conspecific}$	Tree	Tree+Year	Yes	Ash	-0.5	(-.79,.68)
$b_{conspecific}$	Tree+Year	Tree	Yes	Ash	-0.5	(-.79,-.69)
$b_{conspecific}$	Tree+Year	Year	Yes	Ash	0.6	(-.72,.74)
$b_{conspecific}$	Tree	Year	No	Ash	0.8	(-.66,.83)
$b_{conspecific}$	Tree+Year	Tree	No	Ash	-0.4	**(-1.55,-.53)**
$b_{conspecific}$	Tree+Year	Year	No	Ash	0.6	(-.68,.8)
$b_{conspecific}$	Tree+Year	Tree+Year	No	Ash	-0.3	(-.77,.72)
$b_{conspecific}$	Tree	Tree+Year	No	Ash	0.8	(-.67,.83)
$b_{conspecific}$	Tree+Year	Tree+Year	Yes	Ash	0.23	(-.52,.99)
$b_{conspecific}$	Tree	Tree	Yes	Ash	-2.61	**(-2.21,-3.1)**
$b_{conspecific}$	Tree	Tree	No	Ash	-1.48	(-1.97,-.99)
$b_{heterospecific}$	Tree	Year	Yes	Ash	-0.16	(-.88,.54)
$b_{heterospecific}$	Tree	Tree+Year	Yes	Ash	-0.6	(-.81,.69)
$b_{heterospecific}$	Tree+Year	Tree	Yes	Ash	-0.9	(-.83,.66)
$b_{heterospecific}$	Tree+Year	Year	Yes	Ash	-0.11	(-.83,.6)
$b_{heterospecific}$	Tree	Year	No	Ash	-0.14	(-.85,.58)
$b_{heterospecific}$	Tree+Year	Tree	No	Ash	-0.2	(-.76,.72)
$b_{heterospecific}$	Tree+Year	Year	No	Ash	-0.3	(-.75,.7)
$b_{heterospecific}$	Tree+Year	Tree+Year	No	Ash	-0.17	(-.9,.55)
$b_{heterospecific}$	Tree	Tree+Year	No	Ash	-0.21	(-.91,.49)
$b_{heterospecific}$	Tree+Year	Tree+Year	Yes	Ash	0.25	(-.63,.36)
$b_{heterospecific}$	Tree	Tree	Yes	Ash	-0.5	(-.79,.69)
$b_{heterospecific}$	Tree	Tree	No	Ash	-0.47	(-1.21,.27)
b_{year}	Year	Year	Yes	Ash	-1.71	**(-2.21,-1.22)**
b_{year}	Year	Year	No	Ash	-1.3	**(-1.53,-.53)**
b_{year}	Tree+Year	Tree	Yes	Ash	-0.54	**(-1.4,-.4)**
b_{year}	Year	Tree	Yes	Ash	-0.55	**(-1.5,-.6)**

b_{year}	Tree+Year	Year	Yes	Ash	-0.88	**(-1.38,-.38)**
b_{year}	Year	Tree	No	Ash	-0.48	(-.98,.1)
b_{year}	Tree+Year	Tree	No	Ash	-0.43	(-.93,.6)
b_{year}	Tree+Year	Year	No	Ash	-0.61	**(-1.11,-.11)**
b_{year}	Tree+Year	Tree+Year	No	Ash	-0.86	**(-.37,-1.35)**
b_{year}	Tree+Year	Tree+Year	Yes	Ash	-1.3	(-.63,.36)
b_{year}	Year	Tree+Year	Yes	Ash	-0.82	**(-.33,-1.31)**
b_{year}	Year	Tree+Year	No	Ash	-0.57	**(-.8,-1.6)**
$u_{intercept}$	Year	Year	Yes	Ash	4.6	**(3.84,5.47)**
$u_{intercept}$	Year	Year	No	Ash	4.18	**(3.4,4.97)**
$u_{intercept}$	Tree	Year	Yes	Ash	4.32	**(3.53,5.12)**
$u_{intercept}$	Tree	Tree+Year	Yes	Ash	4.51	**(3.63,5.38)**
$u_{intercept}$	Tree+Year	Tree	Yes	Ash	4.35	**(3.51,5.2)**
$u_{intercept}$	Year	Tree	Yes	Ash	4.9	**(3.28,4.89)**
$u_{intercept}$	Tree+Year	Year	Yes	Ash	4.3	**(3.5,5.11)**
$u_{intercept}$	Year	Tree	No	Ash	4.56	**(3.78,5.34)**
$u_{intercept}$	Tree	Year	No	Ash	4.68	**(3.95,5.42)**
$u_{intercept}$	Tree+Year	Tree	No	Ash	3.83	**(3.33,4.32)**
$u_{intercept}$	Tree+Year	Year	No	Ash	3.91	**(3.13,4.69)**
$u_{intercept}$	Tree+Year	Tree+Year	No	Ash	4.43	**(3.68,5.17)**
$u_{intercept}$	Tree	Tree+Year	No	Ash	4.14	**(3.39,4.89)**
$u_{intercept}$	/	/	No	Ash	3.96	**(3.18,4.74)**
$u_{intercept}$	Tree+Year	Tree+Year	Yes	Ash	4.18	**(3.38,4.97)**
$u_{intercept}$	Year	Tree+Year	Yes	Ash	3.48	**(2.61,4.34)**
$u_{intercept}$	Tree	Tree	Yes	Ash	6.19	**(5.54,6.83)**
$u_{intercept}$	Year	Tree+Year	No	Ash	3.4	**(2.32,3.75)**
$u_{intercept}$	Tree	Tree	No	Ash	6.29	**(5.64,6.93)**
u_{tree}	Tree	Tree+Year	Yes	Ash	-0.6	(-1.56,1.43)
u_{tree}	Tree+Year	Tree	Yes	Ash	-0.5	(-1.45,1.35)
u_{tree}	Year	Tree	Yes	Ash	-0.2	(-1.33,1.28)
u_{tree}	Year	Tree	No	Ash	0.6	(-1.12,1.26)
u_{tree}	Tree+Year	Tree	No	Ash	0.3	(-.57,.64)
u_{tree}	Tree+Year	Year	No	Ash	-0.14	(-0.72,0.45)
u_{tree}	Tree+Year	Tree+Year	No	Ash	-0.7	(-1.25,1.11)
u_{tree}	Tree+Year	Tree+Year	Yes	Ash	-0.2	(-1.4,1.36)
u_{tree}	Year	Tree+Year	Yes	Ash	-0.1	(-1.68,1.47)
u_{tree}	Tree	Tree	Yes	Ash	-1.1	(-.5,.5)
u_{tree}	Year	Tree+Year	No	Ash	-0.1	(-1.15,1.12)
u_{tree}	Tree	Tree	No	Ash	-0.79	(-1.73,.15)
u_{year}	Year	Year	Yes	Ash	-0.65	(-1.4,.8)
u_{year}	Year	Year	No	Ash	-0.39	(-1.12,.33)
u_{year}	Tree	Year	Yes	Ash	0.2	(-.71,.75)
u_{year}	Tree	Tree+Year	Yes	Ash	-0.2	(-.84,81)

Table 2.6 continued

u_{year}	Tree+Year	Year	Yes	Ash	-0.27	(-1,.46)
u_{year}	Tree	Year	No	Ash	-0.88	(-1.61,-.15)
u_{year}	Tree+Year	Tree+Year	No	Ash	-0.2	(-.76,.71)
u_{year}	Tree	Tree+Year	No	Ash	-0.4	(-1.15,.34)
u_{year}	Tree+Year	Tree+Year	Yes	Ash	-0.25	(-1.4,.53)
u_{year}	Year	Tree+Year	Yes	Ash	0.99	(.25,1.74)
u_{year}	Year	Tree+Year	No	Ash	0.78	(.7,1.5)
$p_{intercept}$	Year	Year	Yes	Ash	-0.74	**(-1.46,-.2)**
$p_{intercept}$	Year	Year	No	Ash	-0.81	**(-1.44,-.19)**
$p_{intercept}$	Tree	Year	Yes	Ash	-0.93	**(-1.59.-.28)**
$p_{intercept}$	Tree	Tree+Year	Yes	Ash	-0.15	(-.73,.41)
$p_{intercept}$	Tree+Year	Tree	Yes	Ash	-0.59	(1.12,-.6)
$p_{intercept}$	Year	Tree	Yes	Ash	-0.56	**(-1.8,-.4)**
$p_{intercept}$	Tree+Year	Year	Yes	Ash	-0.96	**(-1.17,-.21)**
$p_{intercept}$	Year	Tree	No	Ash	-0.97	**(-1.81,--.12)**
$p_{intercept}$	Tree	Year	No	Ash	0.27	(-.36,.91)
$p_{intercept}$	Tree+Year	Tree	No	Ash	-0.7	(-.69,.53)
$p_{intercept}$	Tree+Year	Year	No	Ash	-0.8	**(-1.61,-.54)**
$p_{intercept}$	Tree+Year	Tree+Year	No	Ash	0.39	(-.23,1.1)
$p_{intercept}$	Tree	Tree+Year	No	Ash	0.17	(-.42,.77)
$p_{intercept}$	/	/	No	Ash	-1.19	**(-1.77,-.61)**
$p_{intercept}$	Tree+Year	Tree+Year	Yes	Ash	0.76	(.16,1.35)
$p_{intercept}$	Year	Tree+Year	Yes	Ash	0.39	(-.17,.95)
$p_{intercept}$	Tree	Tree	Yes	Ash	0.42	(-.16,.97)
$p_{intercept}$	Year	Tree+Year	No	Ash	-0.1	(-.49,.46)
$p_{intercept}$	Tree	Tree	No	Ash	0.56	(-.6,1.18)
p_{tree}	Tree	Tree+Year	Yes	Ash	-0.21	(-1.5,1.62)
p_{tree}	Tree+Year	Tree	Yes	Ash	-0.2	(-.98,.57)
p_{tree}	Year	Tree	Yes	Ash	-0.17	(-.94,.59)
p_{tree}	Year	Tree	No	Ash	0.7	(-1.3,1.45)
p_{tree}	Tree+Year	Tree	No	Ash	-0.54	(-.66,.86)
p_{tree}	Tree+Year	Year	No	Ash	0.9	(-1.8,0.85)
p_{tree}	Tree+Year	Tree+Year	No	Ash	-0.7	(-.97,.82)
p_{tree}	Tree+Year	Tree+Year	Yes	Ash	-0.15	(-1.6,.75)
p_{tree}	Year	Tree+Year	Yes	Ash	-0.27	(-1.7,.51)
p_{tree}	Tree	Tree	Yes	Ash	-0.22	
p_{tree}	Year	Tree+Year	No	Ash	-0.8	(-.83,.67)
p_{tree}	Tree	Tree	No	Ash	-0.1	(-.85,.83)
p_{year}	Year	Year	Yes	Ash	-1	**(-1.47,-.53)**
p_{year}	Year	Year	No	Ash	-0.97	**(-1.42,-.52)**
p_{year}	Tree	Year	Yes	Ash	-0.25	(-.84,.34)
p_{year}	Tree	Tree+Year	Yes	Ash	-0.56	**(-1.5,-.6)**
p_{year}	Tree+Year	Year	Yes	Ash	-0.69	**(-.21,-1.16)**

p_{year}	Tree	Year	No	Ash	-0.21	
p_{year}	Tree+Year	Year	No	Ash	-0.78	**(-1.22,-.33)**
p_{year}	Tree+Year	Tree+Year	No	Ash	-1.37	**(-1.92,-.83)**
p_{year}	Tree	Tree+Year	No	Ash	-2.21	**(-2.65,-1.77)**
p_{year}	Tree+Year	Tree+Year	Yes	Ash	-1.8	**(-2.28,-1.38)**
p_{year}	Year	Tree+Year	Yes	Ash	0.9	(-.45,.65)
p_{year}	Year	Tree+Year	No	Ash	-1.28	**(-1.7,-.85)**
w	Year	Year	Yes	Ash	0.3	(-1.18,1.25)
w	Tree	Year	Yes	Ash	0.4	(-1.13,1.22)
w	Tree	Tree+Year	Yes	Ash	0.5	(-1.33,1.43)
w	Tree+Year	Tree	Yes	Ash	0.4	(-1.27,1.36)
w	Year	Tree	Yes	Ash	0.3	(-1.2,1.26)
w	Tree+Year	Year	Yes	Ash	0.4	(-1.15,1.23)
w	Tree+Year	Tree+Year	Yes	Ash	0.2	(-1.24,1.28)
w	Year	Tree+Year	Yes	Ash	-0.5	(-1.44,1.34)
w	Tree	Tree	Yes	Ash	0.8	
$b_{intercept}$	Tree+Year	Tree+Year	No	Sycamore	9.98	**(9.43,1.53)**
$b_{intercept}$	Tree	Tree+Year	No	Sycamore	12.3	**(11.77,12.83)**
$b_{intercept}$	Tree	Tree+Year	Yes	Sycamore	13.7	**(13.17,14.23)**
$b_{intercept}$	Tree+Year	Year	Yes	Sycamore	12.76	**(12.23,13.29)**
$b_{intercept}$	Tree	Year	No	Sycamore	12.4	**(11.91,12.89)**
$b_{intercept}$	Tree+Year	Year	No	Sycamore	1.76	**(1.23,11.29)**
$b_{intercept}$	Tree+Year	Tree+Year	Yes	Sycamore	9.79	**(9.3,1.28)**
$b_{intercept}$	Tree+Year	Tree	No	Sycamore	1.4	**(9.55,1.53)**
$b_{intercept}$	Tree+Year	Tree	Yes	Sycamore	1.6	**(9.57,1.55)**
$b_{intercept}$	Year	Tree	No	Sycamore	1.1	**(9.48,1.54)**
$b_{intercept}$	Year	Tree	Yes	Sycamore	9.69	**(9.16,1.22)**
$b_{intercept}$	Year	Tree+Year	No	Sycamore	1.8	**(9.59,1.57)**
$b_{intercept}$	Year	Tree+Year	Yes	Sycamore	9.81	**(9.32,1.3)**
$b_{intercept}$	Tree	Year	Yes	Sycamore	12.9	**(12.41,13.39)**
$b_{intercept}$	Year	Year	No	Sycamore	11.39	**(1.9,11.88)**
$b_{intercept}$	Year	Year	Yes	Sycamore	9.59	**(9.2,1.16)**
$b_{intercept}$	Tree	Tree	No	Sycamore	11.46	**(1.97,11.95)**
$b_{intercept}$	Tree	Tree	Yes	Sycamore	9.92	**(9.39,1.45)**
$b_{intercept}$	/	/	No	Sycamore	11.2	**(1.67,11.73)**
$b_{conspecific}$	Tree+Year	Tree+Year	No	Sycamore	9.98	**(9.43,1.53)**
$b_{conspecific}$	Tree	Tree+Year	No	Sycamore	12.3	**(11.77,12.83)**
$b_{conspecific}$	Tree	Tree+Year	Yes	Sycamore	13.7	**(13.17,14.23)**
$b_{conspecific}$	Tree+Year	Year	Yes	Sycamore	12.76	**(12.23,13.29)**
$b_{conspecific}$	Tree	Year	No	Sycamore	12.4	**(11.91,12.89)**
$b_{conspecific}$	Tree+Year	Year	No	Sycamore	1.76	**(1.23,11.29)**
$b_{conspecific}$	Tree+Year	Tree+Year	Yes	Sycamore	9.79	**(9.3,1.28)**
$b_{conspecific}$	Tree+Year	Tree	No	Sycamore	1.4	**(9.55,1.53)**

$b_{conspecific}$	Tree+Year	Tree	Yes	Sycamore	1.6	**(9.57,1.55)**
$b_{conspecific}$	Tree	Year	Yes	Sycamore	12.9	**(12.41,13.39)**
$b_{conspecific}$	Tree	Tree	No	Sycamore	11.46	**(1.97,11.95)**
$b_{conspecific}$	Tree	Tree	Yes	Sycamore	9.92	**(9.39,1.45)**
$b_{heterospecific}$	Tree+Year	Tree+Year	No	Sycamore	(-.21,.97)	-0.59
$b_{heterospecific}$	Tree	Tree+Year	No	Sycamore	(-.16,1.1)	-0.91
$b_{heterospecific}$	Tree	Tree+Year	Yes	Sycamore	**(.31,1.61)**	-2.83
$b_{heterospecific}$	Tree+Year	Year	Yes	Sycamore	**(.35,1.65)**	-0.49
$b_{heterospecific}$	Tree	Year	No	Sycamore	**(.42,1.6)**	-0.77
$b_{heterospecific}$	Tree+Year	Year	No	Sycamore	(-.58,.64)	-0.49
$b_{heterospecific}$	Tree+Year	Tree+Year	Yes	Sycamore	(-.53,.57)	-0.46
$b_{heterospecific}$	Tree+Year	Tree	No	Sycamore	(-.58,.6)	-0.4
$b_{heterospecific}$	Tree+Year	Tree	Yes	Sycamore	(-.61,.69)	-0.49
$b_{heterospecific}$	Tree	Year	Yes	Sycamore	(-.62,.64)	-0.63
$b_{heterospecific}$	Tree	Tree	No	Sycamore	**(.22,1.4)**	-0.69
$b_{heterospecific}$	Tree	Tree	Yes	Sycamore	**(.1,1.19)**	-0.14
b_{year}	Tree+Year	Tree+Year	No	Sycamore	2.41	**(1.88,2.94)**
b_{year}	Tree+Year	Year	Yes	Sycamore	1.93	**(1.4,2.46)**
b_{year}	Tree+Year	Year	No	Sycamore	1.76	**(1.25,2.27)**
b_{year}	Tree+Year	Tree+Year	Yes	Sycamore	2.78	**(2.37,3.19)**
b_{year}	Tree+Year	Tree	No	Sycamore	2.22	**(1.69,2.75)**
b_{year}	Tree+Year	Tree	Yes	Sycamore	2.34	**(1.81,2.87)**
b_{year}	Year	Tree	No	Sycamore	2.29	**(1.76,2.82)**
b_{year}	Year	Tree	Yes	Sycamore	2.29	**(1.76,2.82)**
b_{year}	Year	Tree+Year	No	Sycamore	2.26	**(1.79,2.73)**
b_{year}	Year	Tree+Year	Yes	Sycamore	2.11	**(1.58,2.64)**
b_{year}	Year	Year	No	Sycamore	0.22	(-.31,.75)
b_{year}	Year	Year	Yes	Sycamore	2.1	**(1.48,2.54)**
$u_{intercept}$	Tree+Year	Tree+Year	No	Sycamore	3.35	**(2.64,4.6)**
$u_{intercept}$	Tree	Tree+Year	No	Sycamore	5.1	**(4.52,5.5)**
$u_{intercept}$	Tree	Tree+Year	Yes	Sycamore	5.83	**(5.34,6.32)**
$u_{intercept}$	Tree+Year	Year	Yes	Sycamore	3.87	**(3.36,4.38)**
$u_{intercept}$	Tree	Year	No	Sycamore	4.26	**(3.63,4.89)**
$u_{intercept}$	Tree+Year	Year	No	Sycamore	3.48	**(2.48,4.48)**
$u_{intercept}$	Tree+Year	Tree+Year	Yes	Sycamore	3.85	**(3.12,4.58)**
$u_{intercept}$	Tree+Year	Tree	No	Sycamore	2.69	**(2.8,3.3)**
$u_{intercept}$	Tree+Year	Tree	Yes	Sycamore	2.61	**(2.12,3.1)**
$u_{intercept}$	Year	Tree	No	Sycamore	4.16	**(3.55,4.77)**
$u_{intercept}$	Year	Tree	Yes	Sycamore	3.64	**(3.21,4.7)**
$u_{intercept}$	Year	Tree+Year	No	Sycamore	4.18	**(3.77,4.59)**
$u_{intercept}$	Year	Tree+Year	Yes	Sycamore	3.47	**(3.6,3.88)**
$u_{intercept}$	Tree	Year	Yes	Sycamore	6.3	**(5.42,6.64)**
$u_{intercept}$	Year	Year	No	Sycamore	3.96	**(3.51,4.41)**

$u_{intercept}$	Year	Year	Yes	Sycamore	4.4	**(3.61,4.47)**
$u_{intercept}$	Tree	Tree	No	Sycamore	4.22	**(3.49,4.95)**
$u_{intercept}$	Tree	Tree	Yes	Sycamore	2.41	**(1.96,2.86)**
$u_{intercept}$	/	/	No	Sycamore	3.8	**(3.37,4.23)**
u_{tree}	Tree+Year	Tree+Year	No	Sycamore	0.2	(-1.55,1.59)
u_{tree}	Tree	Tree+Year	No	Sycamore	0.2	(-.74,.78)
u_{tree}	Tree	Tree+Year	Yes	Sycamore	-0.23	(-1.1,.55)
u_{tree}	Tree+Year	Tree+Year	Yes	Sycamore	-0.13	(-.99,.73)
u_{tree}	Tree+Year	Tree	No	Sycamore	-0.1	(-.85,.83)
u_{tree}	Tree+Year	Tree	Yes	Sycamore	-0.1	(-.6,.58)
u_{tree}	Year	Tree	No	Sycamore	-0.5	(-.54,.44)
u_{tree}	Year	Tree	Yes	Sycamore	-0.41	(-.94,.12)
u_{tree}	Year	Tree+Year	No	Sycamore	0.25	(-.24,.74)
u_{tree}	Year	Tree+Year	Yes	Sycamore	-0.1	(-.59,.39)
u_{tree}	Tree	Tree	No	Sycamore	0.13	(-.38,.64)
u_{tree}	Tree	Tree	Yes	Sycamore	0.4	(-.45,.53)
u_{year}	Tree+Year	Tree+Year	No	Sycamore	-0.8	**(-1.23,-.37)**
u_{year}	Tree	Tree+Year	No	Sycamore	-1.41	**(-1.88,-.94)**
u_{year}	Tree	Tree+Year	Yes	Sycamore	-0.42	(-.87,.3)
u_{year}	Tree+Year	Year	Yes	Sycamore	-1.13	**(-1.6,-.66)**
u_{year}	Tree	Year	No	Sycamore	-0.66	**(-1.17,-.15)**
u_{year}	Tree+Year	Year	No	Sycamore	-0.33	(-.74,.8)
u_{year}	Tree+Year	Tree+Year	Yes	Sycamore	0.6	(-.35,.47)
u_{year}	Year	Tree+Year	No	Sycamore	-0.51	(-.94,-.8)
u_{year}	Year	Tree+Year	Yes	Sycamore	-0.44	(-.91,.3)
u_{year}	Tree	Year	Yes	Sycamore	-2.35	(-2.84,-1.86)
u_{year}	Year	Year	No	Sycamore	-0.98	(-1.37,-.59)
u_{year}	Year	Year	Yes	Sycamore	-1.2	(-1.63,-.77)
$p_{intercept}$	Tree+Year	Tree+Year	No	Sycamore	-2.58	**(-3.7,-2.9)**
$p_{intercept}$	Tree	Tree+Year	No	Sycamore	0.6	**(.15,1.5)**
$p_{intercept}$	Tree	Tree+Year	Yes	Sycamore	0.21	(-.24,.66)
$p_{intercept}$	Tree+Year	Year	Yes	Sycamore	-0.62	**(-1.9,-.15)**
$p_{intercept}$	Tree	Year	No	Sycamore	-1.14	**(-1.63,-.65)**
$p_{intercept}$	Tree+Year	Year	No	Sycamore	-0.44	**(-.87,-.1)**
$p_{intercept}$	Tree+Year	Tree+Year	Yes	Sycamore	-2.85	**(-3.34,-2.36)**
$p_{intercept}$	Tree+Year	Tree	No	Sycamore	-1.5	**(-1.54,-.56)**
$p_{intercept}$	Tree+Year	Tree	Yes	Sycamore	-1.21	**(-1.9,-.52)**
$p_{intercept}$	Year	Tree	No	Sycamore	-0.17	(-.66,.32)
$p_{intercept}$	Year	Tree	Yes	Sycamore	-0.52	**(-.99,-.5)**
$p_{intercept}$	Year	Tree+Year	No	Sycamore	-0.4	(-.61,.53)
$p_{intercept}$	Year	Tree+Year	Yes	Sycamore	-0.38	(-.91,.15)
$p_{intercept}$	Tree	Year	Yes	Sycamore	1.59	**(1,2.18)**
$p_{intercept}$	Year	Year	No	Sycamore	-1.94	**(-2.59,-1.29)**

Table 2.6 continued

$p_{intercept}$	Year	Year	Yes	Sycamore	-0.1	(-.59,.39)
$p_{intercept}$	Tree	Tree	No	Sycamore	0.84	**(.31,1.37)**
$p_{intercept}$	Tree	Tree	Yes	Sycamore	-0.11	(-.64,.42)
$p_{intercept}$	/	/	No	Sycamore	0.23	(-.28,.74)
p_{tree}	Tree+Year	Tree+Year	No	Sycamore	0.23	(-.53,.99)
p_{tree}	Tree	Tree+Year	No	Sycamore	-0.23	(-.92,.46)
p_{tree}	Tree	Tree+Year	Yes	Sycamore	0.3	(-.93,.99)
p_{tree}	Tree+Year	Tree+Year	Yes	Sycamore	0.14	(-.57,.85)
p_{tree}	Tree+Year	Tree	No	Sycamore	0.27	(-.32,.86)
p_{tree}	Tree+Year	Tree	Yes	Sycamore	0.28	(-.39,.95)
p_{tree}	Year	Tree	No	Sycamore	0.24	(-.56,1.4)
p_{tree}	Year	Tree	Yes	Sycamore	0.23	(-.55,1.1)
p_{tree}	Year	Tree+Year	No	Sycamore	0.25	(-.57,1.7)
p_{tree}	Year	Tree+Year	Yes	Sycamore	0.27	(-.55,1.9)
p_{tree}	Tree	Tree	No	Sycamore	-0.16	(-1.4,.72)
p_{tree}	Tree	Tree	Yes	Sycamore	0.12	(-.66,.9)
p_{year}	Tree+Year	Tree+Year	No	Sycamore	2.7	**(1.56,2.58)**
p_{year}	Tree	Tree+Year	No	Sycamore	0.4	(-.41,.49)
p_{year}	Tree	Tree+Year	Yes	Sycamore	-0.32	(-.83,.19)
p_{year}	Tree+Year	Year	Yes	Sycamore	0.4	(-.11,.91)
p_{year}	Tree	Year	No	Sycamore	0.79	(.22,1.36)
p_{year}	Tree+Year	Year	No	Sycamore	0.15	(-.34,.64)
p_{year}	Tree+Year	Tree+Year	Yes	Sycamore	2.51	**(2.4,2.98)**
p_{year}	Year	Tree+Year	No	Sycamore	-0.11	(-.6,.38)
p_{year}	Year	Tree+Year	Yes	Sycamore	0.32	(-.9,.73)
p_{year}	Tree	Year	Yes	Sycamore	-1.4	(-1.73,-1.7)
p_{year}	Year	Year	No	Sycamore	2.1	(1.46,2.56)
p_{year}	Year	Year	Yes	Sycamore	-0.6	(-.61,.49)
w	Tree	Tree+Year	Yes	Sycamore	0.7	(-.6,.74)
w	Tree+Year	Year	Yes	Sycamore	-0.5	(-.74,.64)
w	Tree+Year	Tree+Year	Yes	Sycamore	0.3	(-.93,.99)
w	Tree+Year	Tree	Yes	Sycamore	-0.1	(-.77,.75)
w	Year	Tree	Yes	Sycamore	-0.1	(-.78,.78)
w	Year	Tree+Year	Yes	Sycamore	0.1	(-1,1)
w	Tree	Year	Yes	Sycamore	0.7	(-1.3,1.17)
w	Year	Year	Yes	Sycamore	0.14	(-.68,.96)
w	Tree	Tree	Yes	Sycamore	-0.1	(-.79,.77)
$b_{intercept}$	Year	Tree	No	Birch	15.48	**(14.83,16.13)**
$b_{intercept}$	Tree	Tree	No	Birch	15.42	**(14.77,16.7)**
$b_{intercept}$	Tree+Year	Tree	No	Birch	15.8	**(14.39,15.77)**
$b_{intercept}$	Year	Tree	Yes	Birch	15.9	**(14.44,15.74)**
$b_{intercept}$	Tree	Tree+Year	No	Birch	15.22	**(14.57,15.87)**

$b_{intercept}$	Tree+Year	Tree+Year	No	Birch	15.69	**(15.6,16.32)**
$b_{intercept}$	Tree+Year	Tree	Yes	Birch	14.2	**(13.53,14.87)**
$b_{intercept}$	/	/	No	Birch	15.49	**(14.75,16.23)**
$b_{intercept}$	Tree	Year	No	Birch	14.98	**(14.29,15.67)**
$b_{intercept}$	Year	Year	No	Birch	15.26	**(14.61,15.91)**
$b_{intercept}$	Tree+Year	Year	No	Birch	14.97	**(14.32,15.62)**
$b_{intercept}$	Tree	Tree	Yes	Birch	15.27	**(14.62,15.92)**
$b_{intercept}$	Year	Tree+Year	No	Birch	15.34	**(14.71,15.97)**
$b_{intercept}$	Tree+Year	Tree+Year	Yes	Birch	15.6	**(14.89,16.31)**
$b_{intercept}$	Tree	Tree+Year	Yes	Birch	15.3	**(14.65,15.95)**
$b_{intercept}$	Tree	Year	Yes	Birch	15.68	**(15.3,16.33)**
$b_{intercept}$	Year	Year	Yes	Birch	15.17	**(14.48,15.86)**
$b_{intercept}$	Tree+Year	Year	Yes	Birch	16.23	**(15.64,16.82)**
$b_{intercept}$	Year	Tree+Year	Yes	Birch	15.34	**(14.69,15.99)**
$b_{conspecific}$	Tree	Tree	No	Birch	0.16	(-.68,1)
$b_{conspecific}$	Tree+Year	Tree	No	Birch	0.17	(-.67,1.1)
$b_{conspecific}$	Tree	Tree+Year	No	Birch	0.23	(-.61,1.7)
$b_{conspecific}$	Tree+Year	Tree+Year	No	Birch	0.15	(-.69,.99)
$b_{conspecific}$	Tree+Year	Tree	Yes	Birch	1.6	(.62,2.58)
$b_{conspecific}$	Tree	Year	No	Birch	0.1	(-.76,.96)
$b_{conspecific}$	Tree+Year	Year	No	Birch	0.8	(-.78,.94)
$b_{conspecific}$	Tree	Tree	Yes	Birch	0.24	(-.6,1.8)
$b_{conspecific}$	Tree+Year	Tree+Year	Yes	Birch	0.2	(-.94,.98)
$b_{conspecific}$	Tree	Tree+Year	Yes	Birch	0.8	(-.82,.98)
$b_{conspecific}$	Tree	Year	Yes	Birch	0.28	(-.56,1.12)
$b_{conspecific}$	Tree+Year	Year	Yes	Birch	0.4	(-.8,.88)
$b_{heterospecific}$	Tree	Tree	No	Birch	-0.19	(-1.13,.75)
$b_{heterospecific}$	Tree+Year	Tree	No	Birch	-0.2	(-1.14,.74)
$b_{heterospecific}$	Tree	Tree+Year	No	Birch	-0.18	(-1.14,.78)
$b_{heterospecific}$	Tree+Year	Tree+Year	No	Birch	-0.28	(-1.24,.68)
$b_{heterospecific}$	Tree+Year	Tree	Yes	Birch	-0.27	(-1.35,.81)
$b_{heterospecific}$	Tree	Year	No	Birch	-0.12	(-1.2,.96)
$b_{heterospecific}$	Tree+Year	Year	No	Birch	-0.12	(-1.12,.88)
$b_{heterospecific}$	Tree	Tree	Yes	Birch	-0.1	(-1.2,1)
$b_{heterospecific}$	Tree+Year	Tree+Year	Yes	Birch	-0.7	(-1.15,1.1)
$b_{heterospecific}$	Tree	Tree+Year	Yes	Birch	-0.14	(-1.22,.94)
$b_{heterospecific}$	Tree	Year	Yes	Birch	-0.11	(-1.13,.91)
$b_{heterospecific}$	Tree+Year	Year	Yes	Birch	-0.3	(-1.3,.7)
b_{year}	Year	Tree	No	Birch	0.14	(-.47,.75)
b_{year}	Tree+Year	Tree	No	Birch	0.15	(-.46,.76)
b_{year}	Year	Tree	Yes	Birch	0.14	(-.47,.75)
b_{year}	Tree+Year	Tree+Year	No	Birch	0.25	(-.34,.84)
b_{year}	Tree+Year	Tree	Yes	Birch	0.16	(-.49,.81)

b_{year}	Tree	Year	No	Birch	0.12	(-.51,.75)
b_{year}	Year	Year	No	Birch	0.5	(-.15,1.15)
b_{year}	Tree+Year	Year	No	Birch	0.16	(-.45,.77)
b_{year}	Year	Tree+Year	No	Birch	0.34	(-.25,.93)
b_{year}	Tree+Year	Tree+Year	Yes	Birch	0.3	(-.33,.93)
b_{year}	Year	Year	Yes	Birch	0.28	(-.33,.89)
b_{year}	Tree+Year	Year	Yes	Birch	0.7	(-.6,.74)
b_{year}	Year	Tree+Year	Yes	Birch	0.35	(-.3,1)
$u_{intercept}$	Year	Tree	No	Birch	4.64	**(4.19,5.9)**
$u_{intercept}$	Tree	Tree	No	Birch	4.62	**(4.5,5.19)**
$u_{intercept}$	Tree+Year	Tree	No	Birch	4.19	**(3.6,4.78)**
$u_{intercept}$	Year	Tree	Yes	Birch	4.9	**(4.31,5.49)**
$u_{intercept}$	Tree	Tree+Year	No	Birch	4.18	**(3.59,4.77)**
$u_{intercept}$	Tree+Year	Tree+Year	No	Birch	4.21	**(3.68,4.74)**
$u_{intercept}$	Tree+Year	Tree	Yes	Birch	4.63	**(3.83,5.43)**
$u_{intercept}$	/	/	No	Birch	3.94	**(3.39,4.49)**
$u_{intercept}$	Tree	Year	No	Birch	3.53	**(2.96,4.1)**
$u_{intercept}$	Year	Year	No	Birch	3.44	**(2.87,4.1)**
$u_{intercept}$	Tree+Year	Year	No	Birch	4.28	**(3.71,4.85)**
$u_{intercept}$	Tree	Tree	Yes	Birch	4.73	**(4.2,5.26)**
$u_{intercept}$	Year	Tree+Year	No	Birch	4.7	**(4.11,5.29)**
$u_{intercept}$	Tree+Year	Tree+Year	Yes	Birch	4.5	**(4.5,4.95)**
$u_{intercept}$	Tree	Tree+Year	Yes	Birch	4.23	**(3.78,4.68)**
$u_{intercept}$	Tree	Year	Yes	Birch	4.29	**(3.72,4.86)**
$u_{intercept}$	Year	Year	Yes	Birch	4.11	**(3.56,4.66)**
$u_{intercept}$	Tree+Year	Year	Yes	Birch	4.58	**(4.1,5.15)**
$u_{intercept}$	Year	Tree+Year	Yes	Birch	4.51	**(3.94,5.8)**
u_{tree}	Year	Tree	No	Birch	-0.22	**(-.4,-.4)**
u_{tree}	Tree	Tree	No	Birch	-0.22	(-.46,.2)
u_{tree}	Tree+Year	Tree	No	Birch	-0.23	(-.47,.1)
u_{tree}	Year	Tree	Yes	Birch	-0.29	**(-.53,-.5)**
u_{tree}	Tree	Tree+Year	No	Birch	-0.19	(-.5,.12)
u_{tree}	Tree+Year	Tree+Year	No	Birch	-0.33	**(-.6,-.6)**
u_{tree}	Tree+Year	Tree	Yes	Birch	-0.24	(-.57,.9)
u_{tree}	Tree+Year	Year	No	Birch	-0.39	**(-.61,-.17)**
u_{tree}	Tree	Tree	Yes	Birch	-0.15	(-.39,.9)
u_{tree}	Year	Tree+Year	No	Birch	-0.18	(-.38,.2)
u_{tree}	Tree+Year	Tree+Year	Yes	Birch	-0.22	**(-.42,-.2)**
u_{tree}	Tree	Tree+Year	Yes	Birch	-0.4	**(-.65,-.15)**
u_{tree}	Year	Tree+Year	Yes	Birch	-0.24	(-.48,0)
u_{year}	Tree	Tree+Year	No	Birch	0.3	(-.23,.83)
u_{year}	Tree+Year	Tree+Year	No	Birch	0.1	(-.48,.5)
u_{year}	Tree	Year	No	Birch	0.5	(-.48,.58)

Table 2.6 continued

u_{year}	Year	Year	No	Birch	0.5	**(.3,.97)**
u_{year}	Tree+Year	Year	No	Birch	-0.4	(-.93,.13)
u_{year}	Year	Tree+Year	No	Birch	0.9	(-.44,.62)
u_{year}	Tree+Year	Tree+Year	Yes	Birch	-0.7	(-.64,.5)
u_{year}	Tree	Tree+Year	Yes	Birch	0.19	(-.38,.76)
u_{year}	Tree	Year	Yes	Birch	0.37	(-.2,.76)
u_{year}	Year	Year	Yes	Birch	0.27	(-.26,.8)
u_{year}	Tree+Year	Year	Yes	Birch	0.27	(-.26,.8)
u_{year}	Year	Tree+Year	Yes	Birch	0.9	(-.42,.6)
$p_{intercept}$	Year	Tree	No	Birch	-0.6	(-.59,.47)
$p_{intercept}$	Tree	Tree	No	Birch	-0.19	(-.74,.36)
$p_{intercept}$	Tree+Year	Tree	No	Birch	-0.9	(-.6,.42)
$p_{intercept}$	Year	Tree	Yes	Birch	-0.3	(-.58,.52)
$p_{intercept}$	Tree	Tree+Year	No	Birch	-0.16	(-.65,.33)
$p_{intercept}$	Tree+Year	Tree+Year	No	Birch	-0.15	(-.72,.42)
$p_{intercept}$	Tree+Year	Tree	Yes	Birch	-0.6	(-.49,.37)
$p_{intercept}$	/	/	No	Birch	-0.18	(-.91,.55)
$p_{intercept}$	Tree	Year	No	Birch	-0.7	(-.6,.46)
$p_{intercept}$	Year	Year	No	Birch	0.7	(-.48,.62)
$p_{intercept}$	Tree+Year	Year	No	Birch	-0.5	(-.52,.42)
$p_{intercept}$	Tree	Tree	Yes	Birch	-0.25	(-.78,.28)
$p_{intercept}$	Year	Tree+Year	No	Birch	-0.25	(-.72,.22)
$p_{intercept}$	Tree+Year	Tree+Year	Yes	Birch	-0.7	(-.81,.67)
$p_{intercept}$	Tree	Tree+Year	Yes	Birch	-0.1	(-.63,.43)
$p_{intercept}$	Tree	Year	Yes	Birch	0.2	(-.51,.55)
$p_{intercept}$	Year	Year	Yes	Birch	0.2	(-.53,.57)
$p_{intercept}$	Tree+Year	Year	Yes	Birch	0.5	(-.48,.58)
$p_{intercept}$	Year	Tree+Year	Yes	Birch	-0.25	(-.78,.28)
p_{tree}	Year	Tree	No	Birch	-0.3	**(-.55,-.5)**
p_{tree}	Tree	Tree	No	Birch	-0.6	**(-.89,-.31)**
p_{tree}	Tree+Year	Tree	No	Birch	-0.11	(-.4,.18)
p_{tree}	Year	Tree	Yes	Birch	-0.4	**(-.69,-.11)**
p_{tree}	Tree	Tree+Year	No	Birch	-0.13	(-.5,.24)
p_{tree}	Tree+Year	Tree+Year	No	Birch	-0.1	(-.41,.21)
p_{tree}	Tree+Year	Tree	Yes	Birch	-0.16	(-.47,.15)
p_{tree}	Tree	Tree	Yes	Birch	-0.7	(-.38,.24)
p_{tree}	Year	Tree+Year	No	Birch	-0.44	**(-.73,-.15)**
p_{tree}	Tree+Year	Tree+Year	Yes	Birch	-0.4	(-.33,.25)
p_{tree}	Tree	Tree+Year	Yes	Birch	-0.3	(-.61,.1)
p_{tree}	Year	Tree+Year	Yes	Birch	-0.44	(-.75,-.13)
p_{year}	Tree	Tree+Year	No	Birch	0.8	(-.61,.77)
p_{year}	Tree+Year	Tree+Year	No	Birch	0.5	(-.66,.76)
p_{year}	Tree	Year	No	Birch	-0.1	(-.74,.72)

p_{year}	Year	Year	No	Birch	-0.2	(-.91,.51)
p_{year}	Tree+Year	Year	No	Birch	0.8	(-.59,.75)
p_{year}	Year	Tree+Year	No	Birch	0.2	(-.65,.69)
p_{year}	Tree+Year	Tree+Year	Yes	Birch	-0.4	(-1.46,.66)
p_{year}	Tree	Tree+Year	Yes	Birch	0.1	(-.77,.79)
p_{year}	Tree	Year	Yes	Birch	0.5	(-.68,.78)
p_{year}	Year	Year	Yes	Birch	-0.25	(-.94,.44)
p_{year}	Tree+Year	Year	Yes	Birch	0.6	(-.59,.71)
p_{year}	Year	Tree+Year	Yes	Birch	0.5	(-.68,.78)
w	Year	Tree	Yes	Birch	0.8	(-.82,.98)
w	Tree+Year	Tree	Yes	Birch	0.1	(-1,1.2)
w	Tree+Year	Tree+Year	Yes	Birch	0.15	(-.87,1.17)
w	Tree	Tree+Year	Yes	Birch	0.12	(-.82,1.6)
w	Tree	Year	Yes	Birch	0.11	(-.87,1.9)
w	Year	Year	Yes	Birch	0.3	(-.64,1.24)
w	Tree+Year	Year	Yes	Birch	0.14	(-.68,.96)
w	Year	Tree+Year	Yes	Birch	0.8	(-.82,.98)

Table 2.7 Parameters of individual models of beech Parameters with 95% CI didn't include zero were marked in bold

Parameter	Fecundity	Dispersal	Path Effect	Species	Value	95% CI
$b_{intercept}$	Heterospecific	conspecific	No	beech	1.6	**(1.21,1.99)**
$b_{intercept}$	Heterospecific	conspecific	Yes	beech	1.9	**(9.66,1.52)**
$b_{intercept}$	Conspecific +Heterospecific	/	Yes	beech	11.54	**(11.15,11.93)**
$b_{intercept}$	Conspecific +Heterospecific	conspecific	No	beech	9.71	**(9.34,1.8)**
$b_{intercept}$	Conspecific	/	Yes	beech	5.99	**(5.3,6.68)**
$b_{intercept}$	Conspecific	/	No	beech	1.41	**(9.92,1.9)**
$b_{intercept}$	Heterospecific	/	No	beech	11.89	**(11.46,12.32)**
$b_{intercept}$	Heterospecific	/	Yes	beech	11.59	**(11.22,11.96)**
$b_{intercept}$	Conspecific +Heterospecific	conspecific	No	beech	1.39	**(9.94,1.84)**
$b_{intercept}$	/	/	No	beech	1.27	**(9.68,1.86)**
$b_{intercept}$	Conspecific	conspecific	Yes	beech	1.35	**(9.96,1.74)**
$b_{intercept}$	Conspecific +Heterospecific	/	No	beech	1.69	**(1.26,11.12)**
$b_{intercept}$	Conspecific +Heterospecific	/	Yes	beech	5.87	**(5.46,6.28)**
$b_{conspecific}$	Conspecific +Heterospecific	/	Yes	beech	0.6	(-.5,1.25)

$b_{conspecific}$	Conspecific +Heterospecific	conspecific	No	beech	-1.1	**(-1.63,-.57)**
$b_{conspecific}$	Conspecific	/	Yes	beech	0.69	(-.5,1.43)
$b_{conspecific}$	Conspecific	/	No	beech	0.5	(-.13,1.13)
$b_{conspecific}$	Conspecific +Heterospecific	/	No	beech	0.22	(-.51,.95)
$b_{conspecific}$	Conspecific +Heterospecific	/	Yes	beech	0.55	(-.8,1.18)
$b_{heterospecific}$	Heterospecific	conspecific	No	beech	0.17	(-.24,.58)
$b_{heterospecific}$	Heterospecific	conspecific	Yes	beech	0.19	(-.28,.66)
$b_{heterospecific}$	Conspecific +Heterospecific	/	Yes	beech	0.4	(-.7,.87)
$b_{heterospecific}$	Conspecific +Heterospecific	conspecific	No	beech	1.4	(1.13,1.67)
$b_{heterospecific}$	Heterospecific	/	No	beech	-0.24	(-.57,.9)
$b_{heterospecific}$	Heterospecific	/	Yes	beech	-0.25	(-.58,.8)
$b_{heterospecific}$	Conspecific +Heterospecific	conspecific	No	beech	0.85	(.5,1.2)
$b_{heterospecific}$	Conspecific +Heterospecific	/	No	beech	-0.5	**(-.93,-.7)**
$b_{heterospecific}$	Conspecific +Heterospecific	/	Yes	beech	0.72	(.29,1.15)
$u_{intercept}$	Heterospecific	conspecific	No	beech	4.67	**(3.45,5.89)**
$u_{intercept}$	Heterospecific	conspecific	Yes	beech	4.27	**(2.88,5.66)**
$u_{intercept}$	Conspecific +Heterospecific	/	Yes	beech	4.62	**(3.37,5.87)**
$u_{intercept}$	Conspecific +Heterospecific	conspecific	No	beech	4.73	**(4.2,5.44)**
$u_{intercept}$	Conspecific	/	Yes	beech	3.48	**(2.68,4.28)**
$u_{intercept}$	Conspecific	/	No	beech	3.84	**(3.6,4.62)**
$u_{intercept}$	Heterospecific	/	No	beech	3.85	**(3.52,4.18)**
$u_{intercept}$	Heterospecific	/	Yes	beech	3.96	**(3.37,4.55)**
$u_{intercept}$	Conspecific +Heterospecific	conspecific	No	beech	5.5	**(4.97,6.3)**
$u_{intercept}$	/	/	No	beech	2.71	**(1.97,3.45)**
$u_{intercept}$	Conspecific	conspecific	Yes	beech	3.69	**(3.6,4.32)**
$u_{intercept}$	Conspecific +Heterospecific	/	No	beech	3.83	**(3.18,4.48)**
$u_{intercept}$	Conspecific +Heterospecific	/	Yes	beech	2.99	**(2.11,3.87)**
u_{tree}	Heterospecific	conspecific	No	beech	-0.27	**(-.47,-.7)**
u_{tree}	Heterospecific	conspecific	Yes	beech	-0.28	**(-.5,-.6)**
u_{tree}	Conspecific +Heterospecific	/	Yes	beech	-0.18	**(-.38,.2)**
u_{tree}	Conspecific +Heterospecific	conspecific	No	beech	-0.6	**(-.78,-.42)**
u_{tree}	Conspecific +Heterospecific	conspecific	No	beech	-1.6	**(-1.82,-1.38)**
u_{tree}	Conspecific	conspecific	Yes	beech	-0.5	**(-.79,-.21)**
$p_{intercept}$	Heterospecific	conspecific	No	beech	-0.48	**(-.91,-.5)**
$p_{intercept}$	Heterospecific	conspecific	Yes	beech	-0.53	**(-.98,-.8)**
$p_{intercept}$	Conspecific +Heterospecific	/	Yes	beech	-0.68	**(-1.11,-.25)**

$p_{intercept}$	Conspecific +Heterospecific	conspecific	No	beech	-0.45	(-.98,.8)
$p_{intercept}$	Conspecific	/	Yes	beech	-0.43	(-.86,0)
$p_{intercept}$	Conspecific	/	No	beech	-1.53	**(-2.2,-1.4)**
$p_{intercept}$	Heterospecific	/	No	beech	-0.23	(-.8,.34)
$p_{intercept}$	Heterospecific	/	Yes	beech	-0.43	(-1.2,.16)
$p_{intercept}$	Conspecific +Heterospecific	conspecific	No	beech	0.8	(-.37,.53)
$p_{intercept}$	/	/	No	beech	-2.38	**(-3.3,-1.73)**
$p_{intercept}$	Conspecific	conspecific	Yes	beech	-3.33	**(-3.76,-2.9)**
$p_{intercept}$	Conspecific +Heterospecific	/	No	beech	-3.27	**(-3.76,-2.78)**
$p_{intercept}$	Conspecific +Heterospecific	/	Yes	beech	-3	**(-3.41,-2.59)**
p_{tree}	Heterospecific	conspecific	No	beech	-0.24	(-.48,0)
p_{tree}	Heterospecific	conspecific	Yes	beech	-0.29	**(-.54,-.4)**
p_{tree}	Conspecific +Heterospecific	/	Yes	beech	-0.27	**(-.49,-.5)**
p_{tree}	Conspecific +Heterospecific	conspecific	No	beech	-0.28	(-.57,.1)
p_{tree}	Conspecific +Heterospecific	conspecific	No	beech	-0.9	**(-1.14,-.66)**
p_{tree}	Conspecific	conspecific	Yes	beech	-0.1	(-.3,.1)
w	Heterospecific	conspecific	Yes	beech	0.5	(-1.62,1.72)
w	Conspecific +Heterospecific	/	Yes	beech	0.8	(-1.63,1.79)
w	Conspecific	/	Yes	beech	0.7	(-.72,.73)
w	Heterospecific	/	Yes	beech	0.7	(-1.21,1.22)
w	Conspecific	conspecific	Yes	beech	0.9	(-.56,.74)
w	Conspecific +Heterospecific	/	Yes	beech	0.8	(-.68,.84)

Discussion

This chapter models the effects of forest tree density on seed production and dispersal of the four main canopy trees in Wytham Wood, a typical English forest. Models with environmental effects generally provided a good fit with the observed seeds data and performed better than standard models. However, the expected effect of tree density on seed production and dispersal are not supported in all species by model averaging results.

Seed production of the tree species studied is known to be very variable, and fecundity could be affected by many factors like water supply, soil condition and management (Atkinson 1992, Harmer 1994, Hilton and Packham 2003). This is reflected both by field observations

and in the best supported models. Estimations of fecundity for three species changed substantially between years, with ash fecundity dropping and sycamore and birch fecundity rising in 2016 compared to 2015.

The hypothesis that neighbouring trees would affect seed production via competition is only supported by the sycamore data, where non-conspecific trees influenced fecundity. Previously it has been shown that sycamore trees in closed canopy produced fewer seeds than in an open environment (Harmer 1994), this study supports that conclusion. However, sycamore does not seem to influence the fecundity of ash. Both sycamore and ash occur at a similar density. The results therefore may suggest unequal competition between the two most abundant species, sycamore and ash. This phenomenon could have important impact in future forest dynamics and have consequences for the coexistence of those two species. Sycamore shows higher mortality during drought than ash and is predicted to be replaced by ash in Wytham Woods (Morecroft et al. 2008, Carey 2015). The effect reported here on sycamore fecundity could accelerate this process. Although the likely effect of ash dieback disease on ash tree populations will have the opposite effect.

Both ash and sycamore had significant changes in fecundity between years according to the model. Climatic factors like temperature and rainfall sometimes are related to the seed reproduction cycle (Kelly and Sork 2002). However, ash experienced a decrease in fecundity in 2016 while sycamore fecundity increased in that year. Both species also occur together on similar soil. This suggests the change in fecundity may be a result of reproduction cycle rather than variation of external climatic factors between years. This result demonstrates how challenging modelling tree fecundity can be given the high variations in tree fecundity and the causes of which are not fully understood.

Of the three wind-dispersed species, effect of tree density on seed dispersal was only supported by birch data. As expected, birch trees in a more crowded environment generally had shorter mean dispersal distance, and a lower chance of dispersing seeds to distant locations. The path effect, the resistance of surrounding trees on the seed dispersal path was

not found in any of three species. The reason why ash and sycamore dispersal were not affected by tree density is unknown. According to previous survey data, mature ash and sycamore are taller than birch. (Evans et al. 2015). So, one possible explanation is that ash and sycamore seeds are released at higher height and experience higher wind speed, which alleviate interception of surrounding trees. In addition, the long-wings of ash and sycamore seeds compared with those of birch may enable them stay at higher height for longer time. The result doesn't mean dispersal of ash and sycamore are not affected by neighbouring tree density. The model averaged parameter showed tree density had negative effect of dispersal distance of both species, but the 95% CI covered zero. Given the sample size in this study is not very large, a larger-scale study may provide solid support to effect of surrounding trees on seed dispersal.

The estimated dispersal distance of sycamore dropped in 2016 compared to 2015, which is possibly related to the high crop of sycamore seeds in 2016. The recorded monthly averaged wind speed at Wytham during the study period in 2016 was 2m/s, slightly lower (28%) than the 2.8m/s recorded in 2015 (UK Environmental Change Network). The lower wind speed will have contributed to the lower dispersal distance but whether it is responsible for the entire difference seems unlikely to be a result of wind speed change. According to my field observation, individual catkins produced more seeds and were heavier during the sycamore masting of 2016. Those heavy clusters of seeds tend to drop close to the source tree. Indeed, clusters or even branches bearing large numbers of sycamore seeds were found in the traps. If this is true, then seed dispersal would also be related to seed production.

The beech dispersal kernel also shows effect of tree density, with a pattern appearing like the wind-dispersed birch and having a mean dispersal distance that dropped with higher conspecific tree density. However beech trees are thought to be dispersed by animals or by gravity (Packham and Thomas 2012), and the mechanism for dispersal is therefore not the same as birch. Wood pigeons were observed feeding on beech mast in the plot. Potentially some seeds were dropped by wood pigeons or other frugivorous birds during feeding. The

result would suggest that the birds are dropping remotely from the tree from which they were harvested. Such a pattern was reported by Herrera et al. (2011) in hawthorn using a similar method. They found hawthorn in grids with higher fruit availability had shorter dispersal distance. Negative density dependent dispersal is also found in animal-dispersed palm *Attalea butyracea* (Jansen et al. 2014)

In the study I only considered one environmental factor and yearly variation in climatic conditions were not explicitly accounted for. However, these results have a good fit to observed data and provided evidence of surrounding environment has effect on tree fecundity and dispersal. The relatively weak weight for individual models and yearly variation found in tree fecundity and dispersal suggests there are other important factors to be considered. In future studies the modelling approach should be extended to consider additional factors, for example, local climate conditions (especially wind), age of tree, genotype and phenotype of tree, and occurrence of animals (insects, birds, mammals) and pathogens. A larger sample size and more extensive measurement of environmental conditions can be used to further increase understanding of tree fecundity and dispersal dynamic in Wytham Woods and forest alike.

Chapter 3 Effect of Light on Diameter Growth Rate of Tree Seedlings at Wytham Woods, UK

Abstract

Light is important for seedling growth, and variation in seedling shade tolerance is expected to be key in tree species coexistence. I measured seedlings diameter growth for three tree species, their light environment and any signs of herbivory. I related seedling diameter growth to light availability via a logistic growth model. The result showed that the growth of seedlings is well explained by light availability. Differences in diameter growth across the light gradient were small among seedlings of these species, i.e. the seedlings had similar shade tolerances as previously reported from saplings. The effect of browsing on seedling growth rate is also not significant despite a high prevalence of signs of herbivory. It is apparent that a study aimed specifically at understanding the role of herbivory in the growth of seedlings is needed in the future.

Introduction

Light is one of the most crucial factors influencing the growth and survival of a plant. The competition for light is a central process driving community changes and dynamics in many ecosystems, especially in closed forests (Valladares and Niinemets 2008). Plants adapt to light conditions via a combination of physiological and morphological traits, but no combination performs optimally over the whole light gradient, e.g. plants with high photosynthetic rates have high growth rates, but in low light they may starve (Bazzaz 1979, Valladares and Niinemets 2008). Thus, plant species differ in their light niches which results in differing relative performances in various light conditions. In turn adult canopy trees with varying light transmission characteristics create a heterogeneous light environment under canopy (Canham et al. 1990, 1994) . For a long time ecologists and foresters have been

classifying trees as shade tolerant and shade intolerant, and consider that differences in shade tolerance is an important mechanism driving forest succession, where shade intolerant pioneer species will be gradually replaced by shade tolerant species if there is no major disturbance (Whitmore 1989, Kobe et al. 1995).

Light's role in juvenile tree growth has been shown in studies on gap dynamic and seedling establishment. Most studies report that the formation of gaps promotes seedling growth, and species differ in their growth responses to light variation(Latham 1992, Reader et al. 1995, Gray and Spies 1996). Moreover, since the 1980s numerous empirical studies have been quantified the growth rate and mortality of trees in response to the light gradient - the 'shade tolerance' of trees. Many of these studies have found a trade-off between high light growth and low light survival in juvenile trees, in both temperate and tropical forests (Kobe et al. 1995, Kobe 1999, Lin et al. 2002, Baraloto et al. 2005, Coomes et al. 2009). This trade-off results in juveniles of shade intolerant species suffering high mortality in low light but having strong growth response in high light, while juveniles of shade tolerant species have higher survival rate in low light but are out-competed in growth by shade intolerant species.

Many argue that the variations in species shade tolerance are important for maintaining diversity and species coexistence. Interspecific differences in shade tolerance and consistent gap dynamics are considered to be the underpinning mechanisms for species coexistence by gap partition theory (Gravel et al. 2010). However the role of gap partition in maintaining diversity remains controversial with studies yielding conflicting results, for example: Schnitzer and Carson (2001) found that gaps increased the diversity of pioneer tree and liana species, while Hubbell et al. (1999) found that gaps did not increase species diversity in a Panama forest and attribute this result to strong recruitment limitation. Brokaw and Busing (2000) have proposed that gaps are mostly filled with chance occupants rather than best adapted species.

Nevertheless, studies with forest models have shown it is crucial to include growth and survival processes in relation with light to make realistic predictions, as species variation in

growth and survival response to light can translate to changes in community composition via competition. Kobe (1995) found that growth and survival processes at juvenile stages of trees were important for models to get results that are close to real forest compositions. Kunstler et al (2009) showed via simulations that initial light conditions strongly influenced species regeneration success, and interspecific differences in species growth at seedling and sapling stages strongly influenced predicted species composition. A species response to light is also not isolated, but interacts with other environmental pressures like herbivory, soil nutrient and water (Valladares and Niinemets 2008). For example, browsing can reduce species growth and obscure the relationship between growth and light (Krueger et al. 2009). With rapid climate change, the interaction between light and climate on tree growth requires special attention. For instance, rising CO_2 levels can alter trees photosynthetic capacities and their growth and survival responses to light (Hättenschwiler 2001). Rising temperature is also changing tree phenology, advancing times for budding and leafing, resulting in longer growing seasons (Walther et al. 2002, Parmesan 2006b). Longer growing seasons can increase the light acquired by trees and enhance their growth. Species also vary in how sensitive they are to changing temperatures which will lead to changes in species composition (Carey 2015).

In this chapter, I investigated the relationships between light and diameter growth in seedling of three common tree species: ash (*Fraxinus excelsior*), beech (*Fagus sylvatica*) and sycamore (*Acer pseudoplatanus*) in Wytham Woods, Oxfordshire, U.K., as part of a project that aims to produce a predictive model for British forests. SORTIE, the model used in this project, classifies juvenile trees into seedings and saplings and I will focus on growth of seedlings. The three species are all considered to be shade tolerant (Hein et al. 2009, Packham et al. 2012, Thomas 2016). Previously, similar growth-light relationship studies have been conducted on saplings of these study species (Petritan et al. 2007, Carey 2015). As far as I am aware, no similar studies have previously been conducted on seedlings, and species response to light can vary between seedling and sapling stages (Kunstler et al. 2009). This study will

help us better understand the role light plays growth at juvenile stage of these three species and is essential for modelling the future community dynamics of the woods. When measuring the diameter of seedlings, I fitted the allometric relationship between seedling diameter and height. This relationship enables the model to update seedling height when they grow in diameter.

Method

Study Site and Seedling Measurement

Field work was carried out in Wytham Woods, Oxfordshire (51° 46 ′ N, 1° 20 ′ W). It covers 400 ha and has been a research site of Oxford University since the 1940s. The woodland compromises ancient semi-natural woodland, naturally generated secondary woodland and plantations (Mihok et al. 2009). The mean annual temperature is 10°C and the mean annual rainfall is 726 mm (Butt et al. 2009). According to surveys of 164 permanent plots across Wytham Woods, ash seedlings are the most abundant species and its proportion is rising, with ash making up 75% of all seedlings in 2012, while beech and oak seedlings are poorly represented in surveys (Kirby et al. 2014).

To collect seedling growth data, I established seven one meter-wide transects in parts of woodland where seedlings were abundant, with transects ranging from 30-100m long. Measurements were made of seedlings (defined as trees between 100 mm and 1350 mm high) along the transects. I also searched open grassland for seedlings of species which were rare in woodland, like oak and birch. Transects were distributed in both semi-natural woodland, secondary woodland and plantations. Seedling height and diameter at 100mm were measured to 0.01mm in June-August of 2015 with a Vernier calliper (Wiha, Germany) and marked with plastic labels. All seedlings were intact at the first measurement. At the same time of year in 2016 and 2017 I relocated, and re-measured all those marked seedlings I could find. Any signs of browsing were recorded.

Seedling Allometry

The relationship between seedling diameter and height was modelled with a linear function:

$H = 0.1 + b\ D100$ **equation 3.1**

Where:

H is the height (m) of seedling

b is the slope

D100 is the diameter (m) of seedling at 10mm height

R^2 of regression between seedling diameter and predicted height was calculated to measure goodness of fit

Light Measurement and Modelling of Seedling Growth

To evaluate the light environment of seedlings, in July 2017 I took hemispherical canopy photos with a digital camera (Canon EOS 6D) at 1m above the seedlings. The canopy photos were analysed with software Gap Light Analyser (Frazer et al. 1999). The software estimates average light transmission over a growing season. Light intensity was calculated as percentage of full light (i.e. light level above the tree canopy) that reached seedling. Changes in diameter between adjacent years were averaged to calculate averaged annual growth rate. To avoid biases associated with comparing growth rate for seedlings of different sizes, the growth used for analyse was calculated as ratio of averaged growth rate and initial diameters of seedlings (relative growth) (Stancioiu and O'Hara 2006).

The relationship between growth rate and light conditions was represented by a logistic model:

$g = a/(1 + e^{(b-cl)})$ **equation 3.2**

Where

l is the light intensity and g is the relative growth

a, *b* and *c* are model parameters

To investigate effect of herbivory on growth rate and specific difference, I used analysis of covariance (ANCOVA) with growth rate as response variable, light intensity as covariate, species, presence of browsing signs and their interactions as factorial independent variables. When there was significant effect of factorial variables found, I used Tukey's HSD post hoc test to compare different levels of factor.

All analyses were done in R 3.4.0 (R Core Team 2015). ANCOVA was carried out with package *car* and the post-hoc test was done with package *lsmeans.*

Results

Ash was the most abundant seedling sampled. Most beech seedlings were found in transects in beech plantations and were rare in other parts of woodlands. Other trees species, like oak, field maple (*Acer campestre* L.) and birch seedlings were also very rare. Oak and birch seedlings were only found in open grass land which is under management using sheep browsing to stop trees regeneration. Therefore, loss of seedlings and labels was severe and insufficient seedlings remained for analysis. The analysis was conducted for three species with sufficient data, these being ash, beech and sycamore.

Seedling Size, Growth Rate Distribution and Allometry

In total I recorded 41 ash seedlings, 22 beech seedlings and 24 sycamore seedlings with light measurement data and growth rate data. The height of seedlings was between 100-1000 mm with median of 219 mm. Most seedlings of ash and beech were small (below 300mm height) while sycamore seedlings spanned a greater range of height (Fig. 3.1). Relative growth (ratio of averaged growth rate and initial diameter of seedlings) ranged from 0 to 0.58. Averaged growth rates for 3 species were 0.14, 0.18 and 0.13 for ash, beech and sycamore respectively (Fig. 3.2). The heights of seedlings are explained well by their diameters. The parameters and shapes of allometry functions were shown in Table 3.1 and Figure.3.3

Table 3.1 Parameters and r^2 of Allometric Functions

Species	*b*	r^2
Ash	67.55	0.86
Beech	61.13	0.94
Sycamore	64.16	0.90

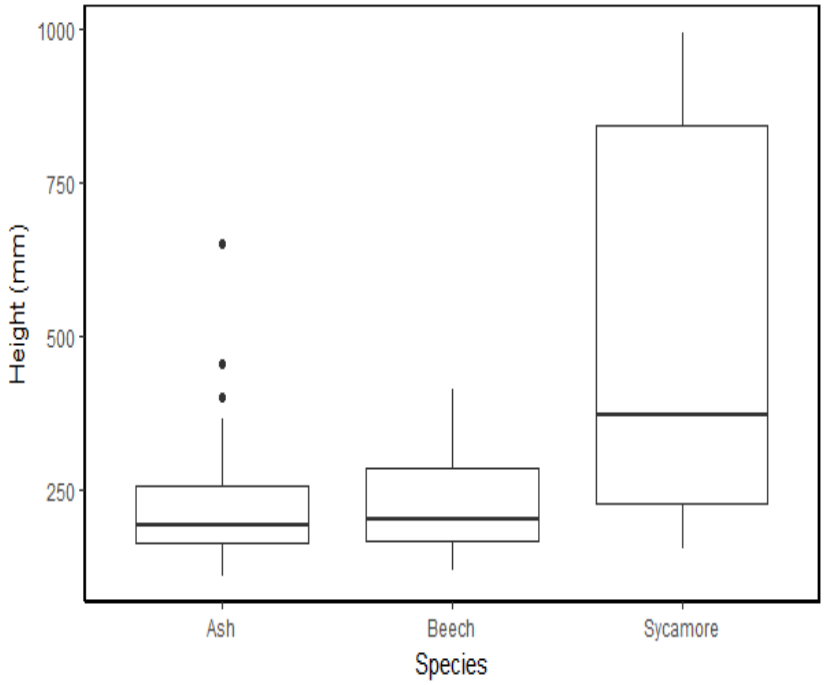

Fig.3.1 Height distribution of seedlings

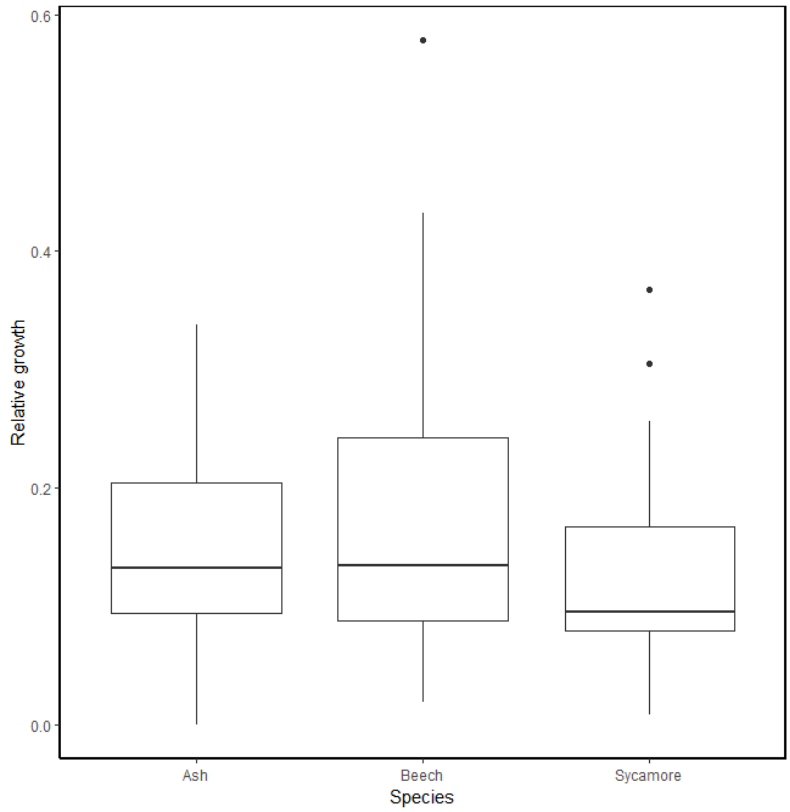

Fig. 3.2 Relative growth of seedling of three species of tree

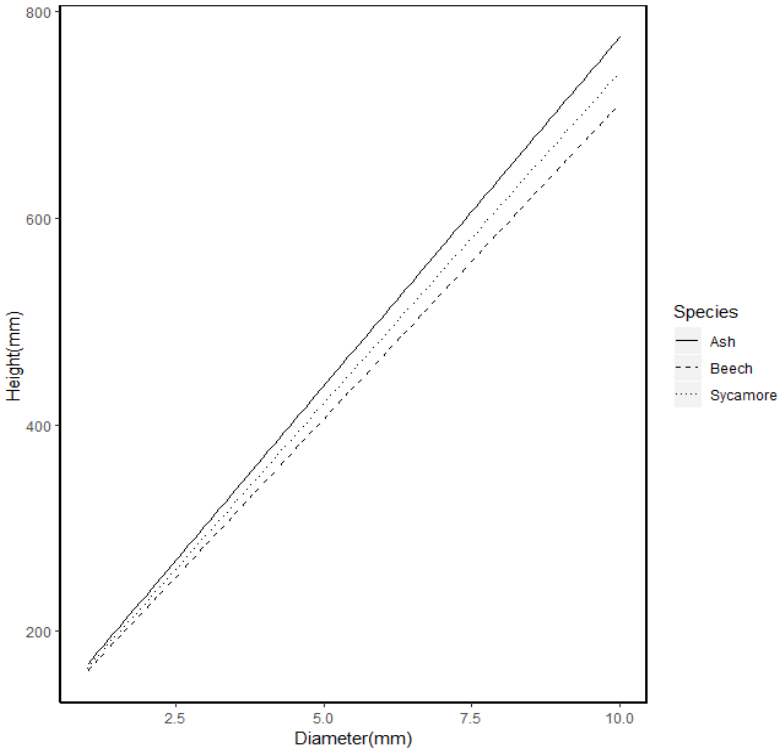

Fig.3.3 Allometric relationships between seedling diameter and height

Light Environment

The light intensity of seedlings as measured using the fish-eye camera (Fig. 3.4) ranged from 9% to 61% (percentage of full light reaching the seedlings), with a median of 30.6%, with most seedlings experiencing 20%-40% of full light (Fig. 3.5).

Fig.3.4. An example of canopy photo

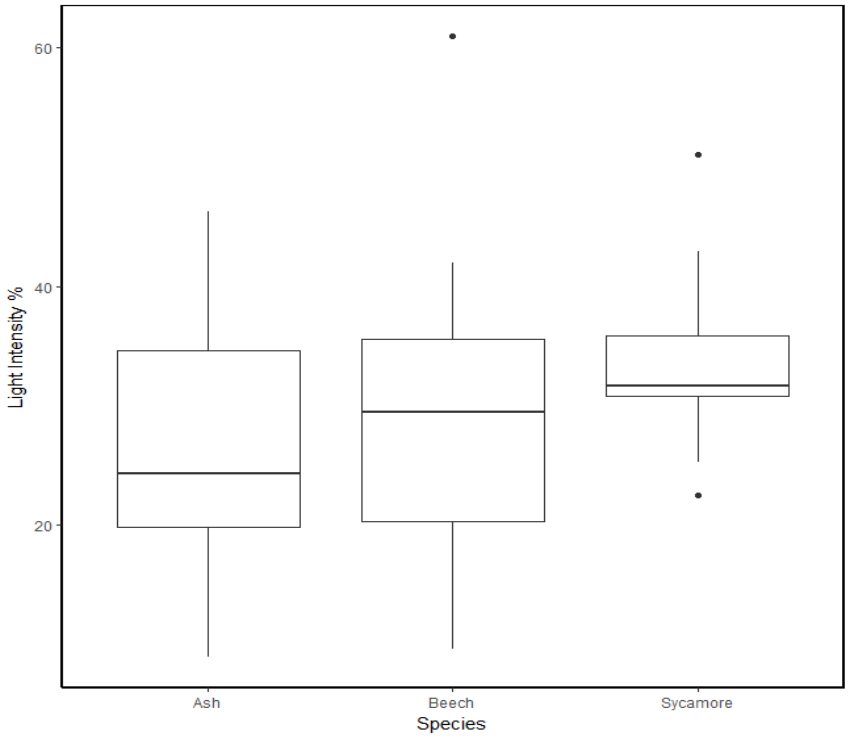

Fig.3.5. Light intensity distributions received by seedlings of three species

Influence of Herbivory

Approximately 40% of analysed seedlings showed signs of herbivory by deer or rabbits on at least one sample occasion. However, there was no significant effect of herbivory on growth rates (ANCOVA, $F_{1,73}$=2.08, p=0.15)

Modelling the Relationship between Light and Seedling Growth

The logistic growth models gave a good fit for the relationship between light intensity and growth rate of the seedlings of these three tree species, explaining 49-70% of variation in growth rates (Table 3.2):

Table 3.2. Parameters and goodness of fit of growth models with 95% confidence intervals in brackets Confidence intervals not containing zero are marked in bold

Species	A	B	C	r^2
Ash	0.35 (**0.11,0.58**)	31.34 (-2.38,65.05)	13.02 (**0.77,25.27**)	0.49
Beech	0.96 (-0.31,2.22)	53.95 (**12.98,94.9**)	14.8 (**3.04,26.56**)	0.7
Sycamore	0.51 (-0.18,1.19)	43.36 (**16.51,70.21**)	8.91 (**1.26,16.55**)	0.55

Growth rates of all three species increased with rising light intensity. Below 30% light intensity, the ranking of growth rate is ash>beech>sycamore. Ash and beech have much higher growth rate than sycamore. Above about 35% light intensity beech acquired the highest growth rate, then Sycamore growth rate surpassed ash above 45% light intensity. However, the difference in relative growth is not large along much of the light gradient (< 0.1, Fig. 3.6). Data from higher light conditions (>50% light intensity) was limited by sampling, so the projection is not presented.

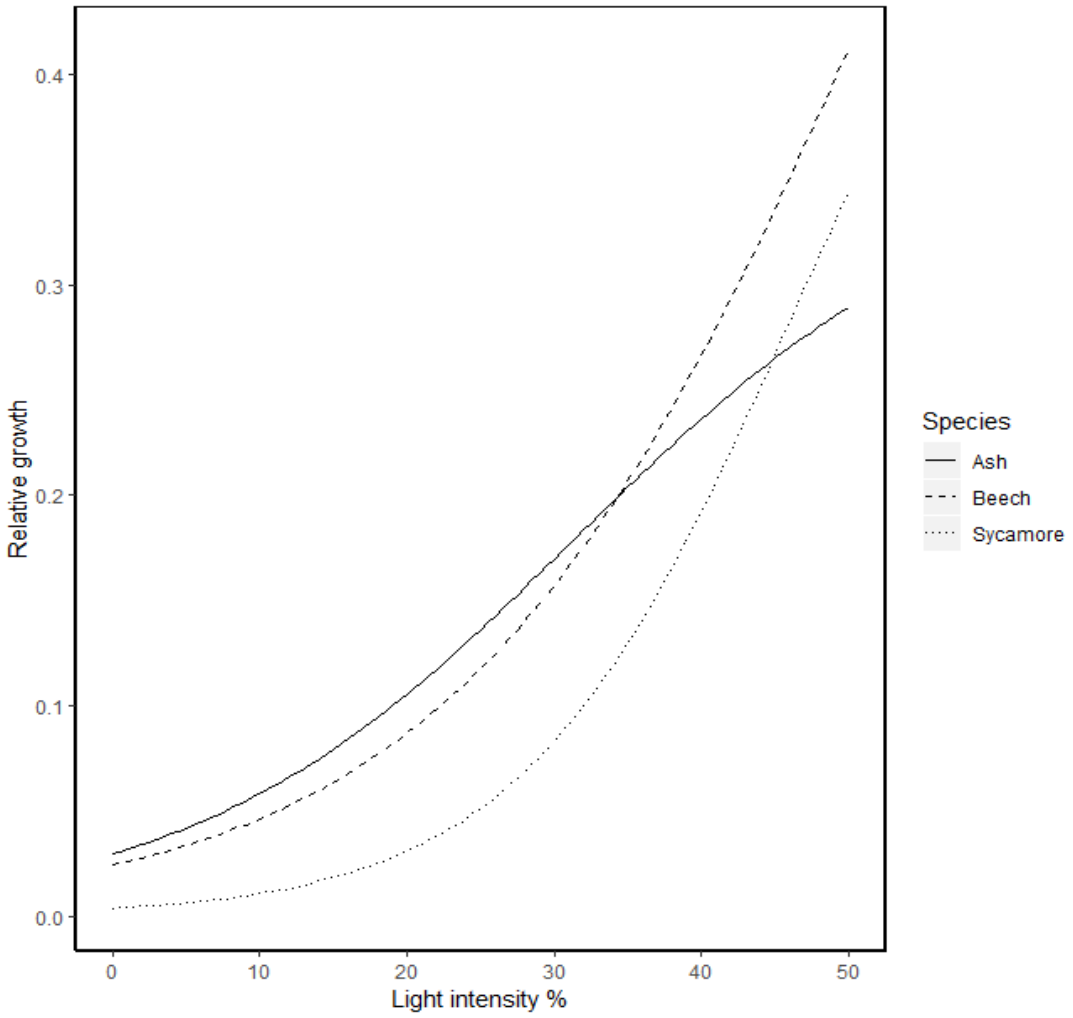

Fig. 3.6. Relationship between relative growth and light condition for three species.

Growth rate comparison between species

ANCOVA showed a significant effect of species on growth rate ($F_{2,73}$=7.66, $p<0.05$), while presence of browsing and its interaction with species were not significant. The post hoc test showed that the growth rates of ash and beech were significantly higher than sycamore ($p<0.01$) while there was no significant difference between ash and beech.

Discussion

Kirby et al. (2014) reported that ash seedlings made up 75% of seedlings in 2012 plot survey across Wytham Wood, while oak and beech seedlings never got to an abundance of >3.5%. This is generally consistent with my sample, of which ash made up 50% of seedlings sampled from naturally regenerated woodlands, while beech and oak seedlings only made up 2%. Therefore, the species composition of my sample seems to reflect that of the woodland as a whole.

Even though the three studied species are all considered to be shade tolerant, logistic models and ANCOVA showed there were specific variations in their growth response to light. The logistic models explained 49%-70% of the variation in growth rate of the three studied species and it is clear that light intensity is an important factor for growth of these tree species. Previous research on these species in Germany showed that height growth of saplings has a similar relationship with light (Petritan et al. 2009). In their study, the order of radial growth rate was beech>sycamore>ash, but the difference was only obvious above 20% light intensity. My result is similar, but the rank order of growth is different. Growth rate of ash and beech are fairly close below 40% light intensity, where they are both higher than sycamore growth rates. But sycamore grew faster than ash above approximately 45% light intensity. The difference between Petritan et al. (2009) in Germany and my study may be caused by factors like different life stages analysed (seedlings here, saplings in Petritan et al. (2009)), and/or site-specific conditions. It is possible that growth rank of species would change with life stage (Kunstler et al. 2009). Wytham Woods also has higher average annual temperature and more uniform rainfall than the Germany site (Butt et al. 2009). The two sites

have quite different species composition, with Wytham co-dominated by ash and sycamore and the Germany site dominated by beech. Differences in various environmental conditions could have led to the different results.

At Wytham Woods, the growth rate of beech was close to that of ash in low light conditions but it grew faster than both ash and sycamore at high light intensity. But the beech seedlings samples were from beech woodland, where other seedling and ground vegetation were scarce. Beech seedlings were rare in mixed stands both in my and previous surveys, which is probably due to the rarity of adult trees as well as competition from other species in mixed woodland.

Ash did not have significant difference in growth rate from beech but there was a small yet significant difference against sycamore according to the post hoc test. The logistic model also predicted ash had slight advantage over sycamore at low to middle light levels. This may contribute to ash's dominance in seedling community. But sycamore may outcompete ash at higher light levels.

Three species of deer occur in Wytham wood : fallow (*Dama dama*), muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) (Morecroft 2001) and in more open areas rabbits may also be found (personal observation). Invertebrate predators could also play important role in herbivory, as some seedlings appeared to be browsed by slugs. The deer population in Wytham Woods increased rapidly since 1980s and is believed to cause changes in vegetation, like declines in shrub species, and a deer control policy is being practiced (Corney et al. 2008). The exact number of deer at Wytham now is estimated to be low (~100) due to management (Savill et al. 2010), but there is still prevalence of browsing damage, observed on 40% of seedlings. However it is surprising that there are no significant effect of browsing on growth rate unlike other studies which found negative effect browsing on seedling growth (Harmer 2002, Krueger et al. 2009). The effect of browsing is affected by the severity and age of seedlings (Gill 1992a). It could be that damage of seedlings by herbivores is not sufficient

to cause a significant effect on sampled seedlings. Consequently, for future studies it would be advantageous to consider also damage severity suffered by seedlings.

Overall our result showed that for the three studied tree species, seedling diameter growth can be well explained by light availability. This provided data basis for predicting seedling growth in heterogenous light environment. Due to logistical reasons and loss of marked seedlings, the sample size used in this study is small. In future a larger scale study would provide more precise estimation of relationship between light and seedling growth.

Chapter 4 Effects of light, size and herbivory on survival of seedlings at Wytham Woods, UK

Abstract

Trees at seedling stages are prone to mortality through various factors, while adult mortality is rare. Thus, studying mortality of tree seedlings is critical for predicting forest regeneration. I used a mark-recapture method to account for bias in field sampling and analyse mortality of seedlings of three tree species in Wytham Woods. I examined the relationship between seedling survival and light intensity, seedling size and herbivory. The results showed ash and beech seedlings are prone to be affected by herbivory while sycamore seedlings survival best explained by size. The results show species specific differences in response to environmental stresses, which have important implications for understanding forest dynamics.

Introduction

Mortality at early life stages is an important process that impacts the age profile of regenerating trees, and drives population dynamics and forest succession (Kobe et al. 1995, Kobe and Coates 1997, Hille Ris Lambers et al. 2005). While adult trees usually have long lifespans and generally low mortality, seedlings and saplings are more easily affected by environment stress factors, and mortality mostly occurs at these early stages (Nakashizuka 2001). As summarized in the last chapter, a trade-off between low light survival and high light growth has been found in many tree communities. Differences in shade tolerance mean that trees have their own regeneration niches along a light gradient. Creation and closure of gaps creates heterogeneous light patterns in forests, and species regenerate in the environment that is most suitable for them. This mechanism is believed to contribute to coexistence of tree species (Kobe 1999, Valladares and Niinemets 2008). The partitioning of regeneration niches

is most obvious between pioneer species and shade-tolerant species, and it is thought that the niches of shade tolerant species can overlap substantially (Brokaw and Busing 2000). Density-dependent mortality is also considered as an important mechanism in maintaining diversity and in determining the spatial pattern of trees (Wright 2002, Lambers et al. 2002, Inman-Narahari et al. 2016). The classical Janzen-Cornell effect describes seedlings near parent trees as being more susceptible to attack by herbivores and pathogens, so negative-density dependent effects shape spatial distribution pattern of trees (Janzen 1970; Connell 1971). Knowledge of tree survival is also important to make predictions for forest dynamics. Many model simulation studies have shown that using specific-mortality functions of juvenile trees is key to producing model simulations close to reality (Kobe et al. 1995, Pacala et al. 1996, Kunstler et al. 2009).

Numerous factors can affect the survival of seedlings. Light is the most important resource for plants to survive and grow and it has received extensive study in trees (see chapter 3). In low light, the carbon capture of seedlings is low and it is harder to maintain a positive carbon balance (Bazzaz 1979). Shade tolerant species usually develop a lower leaf area to biomass ratio to reduce the cost of gas exchange (e.g. respiration), which is considered important for their persistence in low light (Lusk 2004). As discussed in the last chapter, many studies have found clear trade-offs between species low light mortality and high light growth, and it is suggested that interspecific difference in shade tolerance can be important for species coexistence and the community succession (Canham et al. 1994, Kobe and Coates 1997, Kobe 1999, Poorter 1999, Bloor and Grubb 2003). Light affects the growth rate of trees and growth rate has found to be a good indicator of mortality (Wyckoff and Clark 2000). Therefore, studies relating light and mortality of juvenile trees often employ a method to model growth rate with light first, and then model growth rate with mortality to derive, indirectly mortality with light. But this approach requires measuring growth rate of individuals that are alive and growth rate in individuals that have recently died, which is

usually done by taking stem cross sections. However that approach is not suitable for seedlings without woody tissue (Kobe et al. 1995).

Size is also an important factor affecting seedling mortality. Plant responses to environment stress may vary with their size, and the main constraints on seedling survival may change with ontogeny, so survival can be size-dependent (Niinemets 1998). Usually, larger seedlings have access to higher light availabilities and are more resistant to mechanical damage, herbivory, drought and pathogens, resulting in higher survival probability (Niinemets 1998, Lusk 2004). For instance once juvenile trees have reached a certain age they will rarely suffer mortality from browsing by herbivores (Gill and Beardall 2001). But according to Kneeshaw et al. (2006), smaller seedlings of the same species have relatively higher shade tolerance because their ratio of photosynthetic to non-photosynthetic biomass is higher, thus their respiration cost are lower. The study suggests that differences in shade tolerance are most significant between small seedlings, as with seedlings growth, more energy will be allocated to non- photosynthetic tissues and shade tolerance between species will converge. Overall, most studies have found that survival of juvenile trees increases with increasing size (Gilbert et al. 2001, Kunstler et al. 2009). But the size effect is life-stage dependent. Kunstler et al. (2006) showed significant effect of size on mortality of both seedlings and saplings stages, and the size effect was strongest for seedling survival, and Moustakas & Evans (2014) found size-dependent mortality in saplings and adult trees of some tree species.

Herbivory is amongst the most important causes of mortality for seedlings. Moles & Westoby (2004) found that herbivory is the most frequent cause of mortality in a compiled analysis of publications, and this was followed by drought and pathogens. Deer are important herbivores in Wytham Wood as well as in many European forests (Morecroft 2001, Mihok et al. 2009, Gerhardt et al. 2013). Their browsing on juvenile trees has been recognized as an important driver of forest structure change and a factor affecting forest regeneration (Gill and Beardall 2001, Harmer 2002, Gerhardt et al. 2013). The impact of browsing on tree survival can vary with intensity of browsing damage, browser's preference and browsed species resistance (Gill

1992, Gill and Beardall 2001, Tripler et al. 2005). Generally, deer browsing decreases survival of seedlings and reduces their abundance, but studies have shown that seedlings of different species have varied resistance to browsing by various herbivores, and broadleaved trees usually have higher tolerance than conifers (Gill 1992). In some cases, browsing can reduce competition from other trees and ground vegetation, facilitate survival and growth of certain species (Kunzneov 1987, Sykes 1992). Thus, the effect of browsing on forest regeneration is complicated and varies a lot from site to site. Certainly, it is necessary to consider the effects of herbivory when studying seedling mortality.

In field studies, a problem often encountered when estimating seedling survival across time is to identify whether a seedling is dead or overlooked. Even though trees are immobile, at the seedling stage their small size mean that they are easily overlooked, especially in a dense vegetation environment. In addition, dead seedlings are hard to find as they might have been completely consumed by herbivores or decomposed. One way to solve this problem is to adopt a method commonly used in animal ecology studies, the capture-recapture model. The approach can account for imperfect detection rates and provide unbiased estimates of survival rate, and it has been applied successfully on several previous occasions (Shefferson et al. 2003, Shefferson 2006, Moustakas and Evans 2015)

In this chapter, I studied survival rate of seedlings of three common tree species ash, beech and sycamore like the last chapter, in Wytham Woods, UK, using the capture-recapture method. I considered light condition and seedling size as two covariates, which might affect seedling survival probability, due to their importance in various studies. I hypothesize that the inclusion of both factors can improve the survival model significantly. To account for the effect of herbivory, I used a multi-state capture-recapture model, incorporating into the model whether the seedling has been browsed. Herbivory is expected to decrease survival chance of seedlings.

Methods

Seedling data collection

Seedling data were scored in the surveys described in Chapter 3. In brief, labelled seedlings in the transects laid in the wood in June-August 2015 and resurveyed at the same time of year in 2016 and 2017. Seedling diameters at 100mm and light conditions were also measured. Signs of herbivory (e.g. partial leaves and browning apical meristems) were recorded. Seedlings were sampled in both closed canopy and open grassland, however marked seedlings in open grassland suffered severe browsing from sheep and most of them could not be located again. So, this part of data was not included because it did not reflect the natural survival rate of seedlings.

Modelling of survival probability

I used the multi-state mark-recapture model to analyse the data, applying the capture-mark-recapture software package MARK (White and Burnham 1999). The model takes the encounter history of seedlings as input: if a seedling was found intact, without signs of browsing at one sampling occasion, this encounter was encoded as 'N', otherwise if there was browsing it was encoded 'Y'. If it was not found in one survey, then the encounter was scored '0'. So a seedling encoded 'N0Y' means that it has an encounter history not browsed in year one, missed in year two and found browsed in year three. Encoding seedlings as browsed or intact are two states of seedlings, but seedlings can transfer only from the "intact" to "browsed" state. The multi-state model decomposes the encounter probability into three components:

Survival probability S^r_i : the probability of a seedling surviving from sample occasion i to i+1 given the individual was in state r at time i.

Relocation probability p_i : the probability an individual was alive at sampling occasion i and relocated at sampling occasion i+1.

Transition probability $\psi^{rs}{}_i$: the probability of an individual under state *r* at sample occasion *i* is in state *s* at sample occasion *i*+1, given it is alive at *i*+1.

The probability of encounter history 'N0Y', P_{N0Y} then would be:

$S^N{}_1\ \psi^{NN}{}_1(1\text{-}p_1)S^N{}_2\ \psi^{NY}{}_2\ p_2 + S^N{}_1\ \psi^{NY}{}_1(1\text{-}p_1)S^Y{}_2\ \psi^{YY}{}_2\ p_2$, **equation 4.1**

as the seedling has two possible states at the second occasion, when it was not found.

To estimate the effect of light and seedling size on survival probability, I included measurement of diameter at 100mm at the first sampling occasion and light intensity of seedlings as two covariates. Survival probability can vary with seedling size, light intensity and browsing state. The survival probability S is related to covariates with a logit link:

$S = \frac{e^{(\beta_0+\beta_1 x)}}{1+e^{(\beta_0+\beta_1 x)}}$ **equation 4.2**

where

S is the survival probability

β_0 and β_1 are intercept and slope respectively

x is a covariate

Three factors were introduced in modelling of survival probability: light intensity, seedling size and if seedling was browsed. Light is most important resource for seedlings and seedlings should have higher survival probability with increasing light. Larger seedlings are supposed to have higher resistance to browsing and pathogens thus they can have higher survival probability. Browsing is supposed to decrease survival. I hypothesize three factors would be important for species survival. Species-specific shade tolerance and resistance to browsing could lead to difference in survival rate. Beech is considered the most shade-tolerant of these species (Packham et al. 2012) and beech seedlings may survival better in low light condition than ash and sycamore. Possible interaction may exist between factors: Smaller or seedlings with low light availability may be less resistant to herbivory and have higher mortality after

browsed. Thus, models with different combinations of factors and their interactions were fitted.

Transition probability and relocation probability are assumed to be constant across sample occasions. The transition probability from browsed to intact was fixed to 0, as this transition is unrealistic. The are 7 possible encounter history in total. The multinomial log likelihood of acquiring observed encounter history of seedlings is:

$$L=F_{N0Y}ln(P_{N0Y})+F_{N00}ln(P_{N00})+F_{N0N}ln(P_{N0N})+F_{NY0}ln(P_{NY0})+F_{NYY}ln(P_{NYY})+F_{NNN}ln(P_{NNN})+F_{NNY}ln(P_{NNY})$$ **equation 4.3**

Where F is the number of a specific encounter history observed, and P is the probability of encounter history calculated as equation 4.1

The probabilities S, ψ and p are estimated with the Maximum Likelihood method against the observed capture history.

Seedlings are small and exist in dense vegetation, so marked seedlings could be missed in following survey. In fact, even adult trees can be missed in surveys and found afterwards (Moustakas and Evans 2015). The mark-recapture method was used to deal with possible missing seedlings and estimate relocation probability.

A total of 12 models including different combinations of covariates and their interactions plus a model with constant survival probability were fitted using MARK.

Goodness of fit testing and model selection

Model selection process was based on AICc values. The model with the lowest AICc value was considered the best-supported model, although all models with AICc difference between the best-supported models (ΔAICc) $\leq$2 were considered equally parsimonious.

There is no acknowledged conventional method of evaluating goodness-fit of multi-state models. Before building the models I fitted a fully parameterised model where survival, relocation and transition probabilities were allowed to vary freely between sampling

occasions for each species, and estimated an overdispersion parameter c using MARK's bootstrapping function to test if overdispersion exists (Moustakas and Evans 2015). The overdispersion parameters were <1 for each species, suggesting no overdispersion in the data. Therefore, the AICc values were not corrected (Cooch and White 2016).

Results

In total there were 57 ash seedlings, 37 beech seedlings and 34 sycamore seedlings used in the survival analysis (Fig 4.1-4.3). The performance of all models for the three species are presented in Table 4.1 ranked within each species by AICc values. The most well-supported models are in bold.

According to the best-supported models, relocation probabilities of three species are high (>90%). Probabilities of being browsed (transition probabilities from "intact" to "browsed") have a rank of: beech>sycamore>ash (Table 4.2).

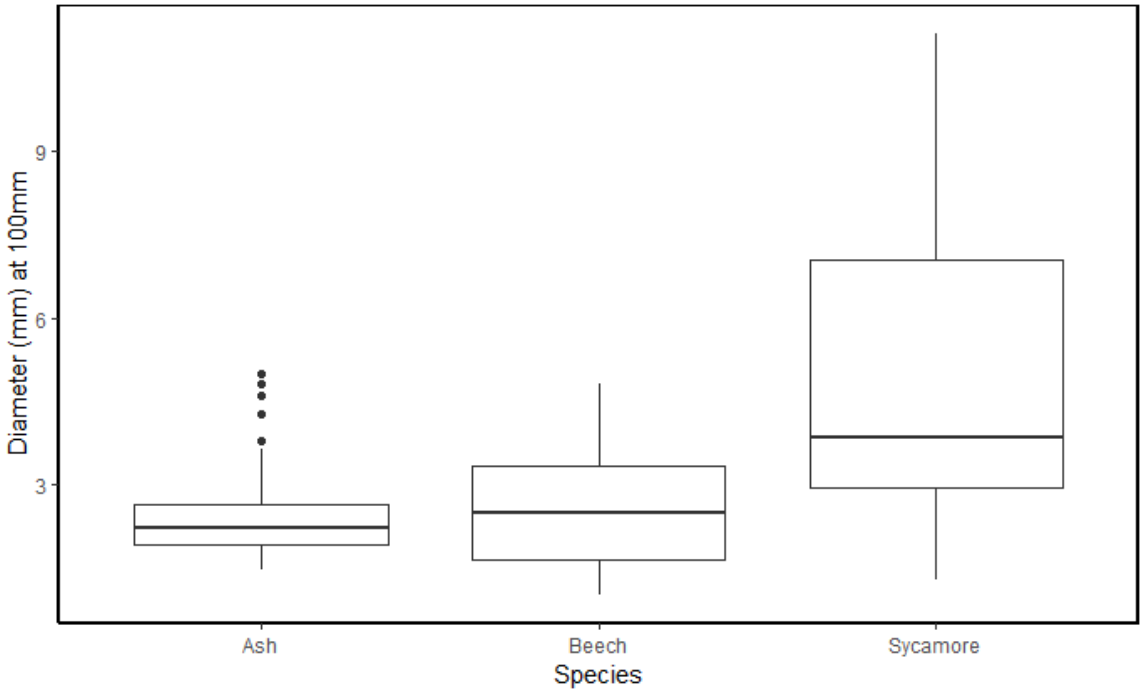

Fig 4.1 Diameter distribution of seedlings

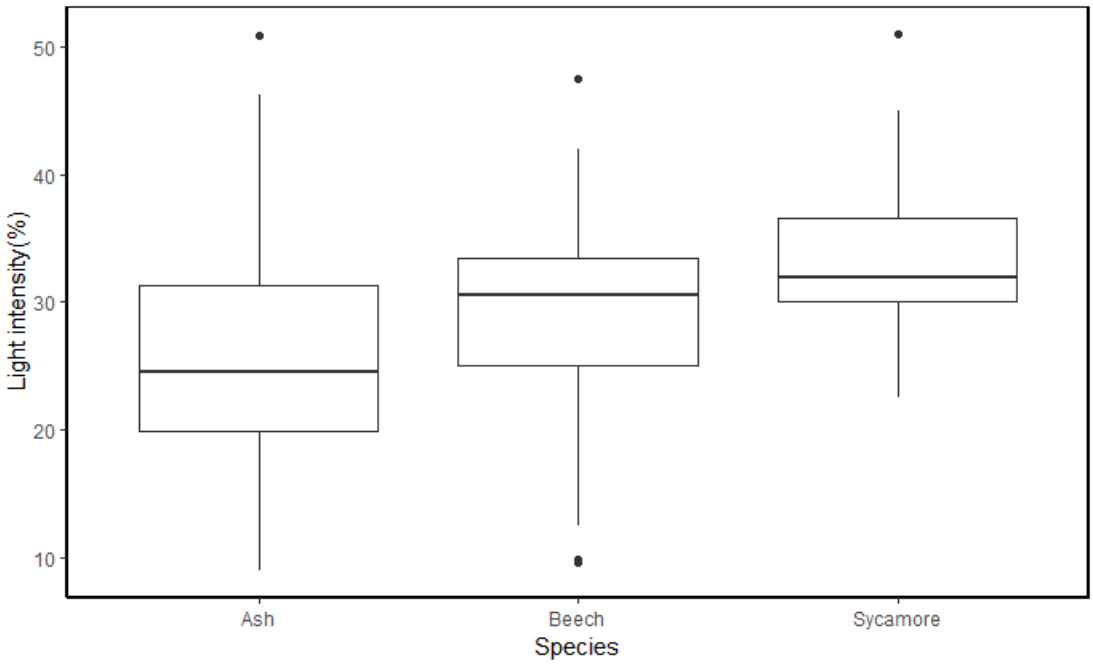

Fig 4.2 Light intensities experienced by the seedlings

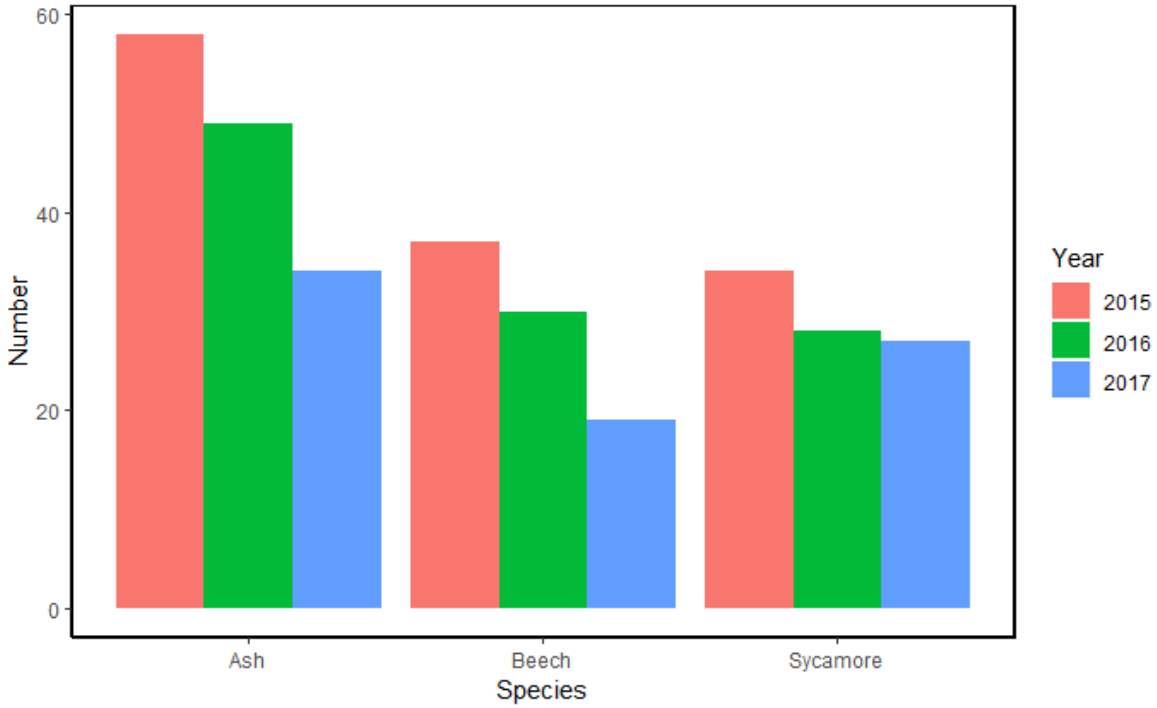

Fig 4.3 Number of sampled seedlings

Table 4.1 AICc values of all models for three species. Light and size represent two continuous variables of light intensity and state represent "browsed" or "intact". The models in bold are equally best-supported models

Species	Model	AICc	Delta AICc
Ash	**State**	**223.06**	**0**
Ash	**light+state**	**223.26**	**0.2**
Ash	**size+light+state**	**224.75**	**1.69**
Ash	**size+state**	**224.87**	**1.81**
Ash	light×state	225.28	2.22
Ash	Constant	225.28	2.22
Ash	size×state	226.68	3.62
Ash	Size	227.42	4.36
Ash	size+light	228.2	5.14
Ash	size×light	230.39	7.33
Ash	Light	230.71	7.65
Ash	size×light×state	233.74	10.68
Sycamore	**Size**	**127.93**	**0**
Sycamore	size×state	129.96	2.03
Sycamore	size+state	130.16	2.23
Sycamore	size+light	130.27	2.34
Sycamore	size+light+state	130.53	2.6
Sycamore	size×light	132.47	4.54
Sycamore	Constant	134.99	7.06
Sycamore	State	137.23	9.3
Sycamore	Light	137.26	9.33
Sycamore	size×light×state	138.17	10.24
Sycamore	light+state	139.5	11.57

Table 4.1 continued

Species	Model	AICc	Delta AICc
Sycamore	light×state	140.01	12.08
Beech	**State**	**146.32**	**0**
Beech	**Constant**	**146.48**	**0.16**
Beech	light+state	148.47	2.15
Beech	size+state	148.54	2.22
Beech	Light	148.68	2.36
Beech	Size	148.76	2.44
Beech	size+light+state	150.71	4.39
Beech	light×state	150.72	4.4
Beech	size×state	150.8	4.48
Beech	size+light	151.05	4.73
Beech	size×light	152.88	6.56
Beech	size×light×state	159.74	13.42

Table 4.2 Relocation and browsing probability estimates from best-supported models

Species	Relocation Probability ±se	Browsing Probability ±se
Ash	0.909±0.050	0.291±0.053
Beech	0.946±0.051	0.528±0.081
Sycamore	0.933±0.038	0.396±0.070

Herbivory alone appeared in the best models of both ash and beech (Table 4.1). As expected, browsed seedlings had lower survival probability than intact seedlings (Fig 4.4). Ash has several models with more-or-less close performances (Table 4.1). Four models were within

delta AICc <2 range. However, herbivory entered each model of ash with delta AICc values <2 and had a negative effect on seedling survival in each case. For beech, the model with constant seedling survival also received equal support with herbivory model. Herbivory also appeared in 2nd and 3rd best models in sycamore but these were not within the delta AICc values <2 range. For ash, four models were in delta AICc <2 range, and all three covariates appeared in these models.

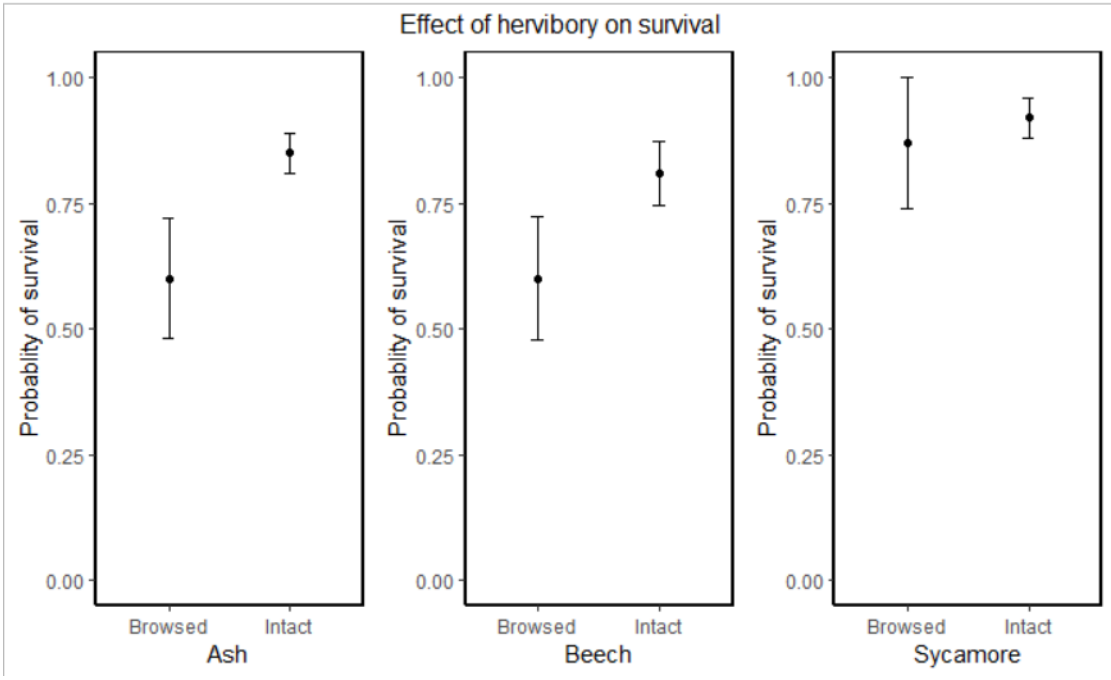

Fig.4.4 Comparison of estimated annual survival probability between browsed and intact seedlings from herbivory model Bars represent standard errors.

Seedling size best predicted survival of sycamore (Table 4.2). Seedling size has a positive effect on survival probability. Sycamore Seedlings have low survival probability when they have a small size, but survival increases dramatically as they get larger, approaching 100% at 5mm diameter (Fig.4.5). Other models were not in delta AICc ≤2 range.

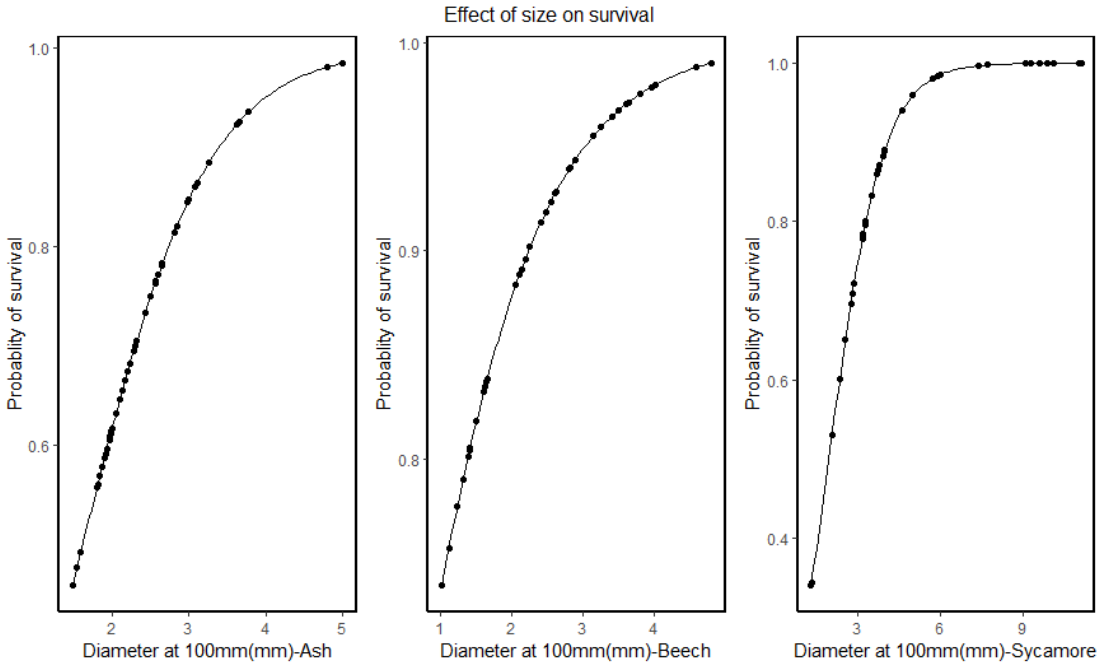

Fig.4.5 Relationships of seedling size and annual survival probability estimated by the size model

Discussion

I estimated survival probabilities of three common tree species, ash, sycamore and beech and explored the effects of light, seedling size and herbivory on seedling survival. Even though all three species are shade-tolerant at seedling stage, there are differences in their response to environment factors, which may have important implications on dynamic of forest.

Light intensity, though expected to be the most important resource for seedling growth, was only amongst the most well-supported survival models for ash in combination with other covariates. In this species, the model with lowest AICc showed browsed seedlings had lower survival probability than intact seedlings (Fig.4.4). As expected, higher light intensity increased seedling survival rate in other models for ash. For beech and sycamore, the best models did not have an effect of light. This result could be attributed to both these species being shade tolerant. However, ash is also considered to be shade tolerant. Perhaps the differential responses to light intensity arises because of different degrees of shade tolerance. Beech is considered to be very shade-tolerant, whilst ash and sycamore as intermediate shade-tolerant (Packham et al. 2012, Thomas 2016). However sycamore is also considered to be

more shade tolerant than ash (Packham et al. 2012). Niinemets and Valladares (2006) quantified shade tolerance for woody species on a 0-5 scale from low to high tolerance, with ash having lowest shade tolerance (2.66) compared to beech (4.56) and sycamore (3.73). The relatively low shade tolerance might explain why light was more important in survival models of ash. On the other hand, the light availability at our study site was relatively high. Average light intensity of sycamore and beech, and ash in our sample were 33.07%, 28.71%, and 24.6% of full light intensities. Only a few ash and beech seedlings experienced light intensity <10%. According to a study in Germany, mortalities of saplings of these species were close to zero at above 15% light (Petritan et al. 2007). So light is also probably not low enough to be a limiting factor for survival for most of the sampled seedlings. Combined with result of growth in relation to light in last chapter, there is not strong evidence of trade-off between low light survival and high light growth. Though species growth rates were well explained by light, only the survival of ash appeared to be affected by light. However, Petritan et al. (2007) did find trade-offs in saplings of these three species with beech having the lowest mortality in low light and slowest growth in high light. The different findings reported here could suggest that shade tolerances of the studied species were more similar at seedling stage. Another reason the trade-off was not present here could be herbivory, or another factor not accounted for that influenced the survival of the seedlings, like competition from other seedlings and vegetation, soil nutrient, and rainfall altered the relationship between growth and survival (Long et al. 2007).

Previous studies have found browsing could change species rank in survival and growth studies (Tripler et al. 2005, Krueger et al. 2009). Browsing is an important driver of forest change in Wytham Woods. It is believed that rising deer populations between the 1970s-1990s led to a decrease in ground shrubs and restricted tree regeneration. However, since 1990s deer management may have led to signs of recovery in vegetation, such as an increase in ash saplings (Mihok et al. 2009, Kirby et al. 2014). In my results, seedlings still had high probability of being browsed by deer and other herbivores and browsing has an effect on

survival of some species(Table 4.1 and 4.2). According to the model used here, herbivory is most important for explaining survival of ash as it was included in every top ranked model. In the best model of ash, herbivory had an interaction with light on survival. Herbivory also occurred in beech's best fit model but the model with constant survival probability was equally well supported ($\Delta AICc<2$). However, sycamore survival was not affected by browsing. Studies on resistance of these species' seedlings to browsing are few, but Harmer (2002) who simulated browsing using controlled clipping of seedlings showed that ash and sycamore seedling survival was significantly reduced by simulated browsing, while beech seedlings were unaffected. Harmer (2002) found that damage through simulated browsing was usually more severe than natural browsing. However, damage from natural browsing varies a lot between different seedlings and this might result in different results between simulated browsing and a field study. The results presented here suggest that sycamore has higher resistance than ash and beech to browsing. However, I only used browsed/not browsed as an indicator of browsing, and a more refined measure of browsing might prove to be fruitful in further investigation. Nevertheless, the result shows there are some difference in species responses to browsing on survival, and to promote regeneration of ash and beech, current deer management should be continued or enhanced. Surprisingly though, there was no significant difference between the growth rates of browsed and not browsed seedlings, even though browsing did have effect on survival of ash and beech. The reason could be that compensatory growth made up biomass loss of browsing, as deciduous tree species are considered to have high compensatory ability (Hester et al. 2004). Besides, the exact timing that browsing happened was unknown, so browsing could have happened after the growing season was over.

The results also provide some evidence that larger seedling sizes promote seedling survival. Size appeared in two of the top models for ash and it alone was the best predictor of sycamore survival. In these models an increase in seedling size had positive effect on survival of seedlings. This is consistent with most studies on seeding survival. For example, Moustakas

and Evans (2015) found that survival rates of ash, sycamore and beech to increase with their DBH at all life stages (sapling and adult) at the same study site. Together with my study this shows size has life stage specific effect on survival of some tree species like ash and sycamore, but the relationship is less clear in beech seedlings.

There are still some potentially important factors like soil nutrients, soil moisture and competition from other seedlings and ground vegetation which were not included in the model and the study period was also short, occurring over only two growing seasons. In this study I only sampled seedlings higher than> 100mm. As smaller seedlings tend to be even less resistant to herbivory and pathogen, the survival estimate would probably be lower if these very young seedlings were included. However, the results showed species-specific difference in survival rates and suggests differences in shade tolerance and herbivory resistance, which may have implications on the future dynamics of forests. Even though ash seedlings are most abundant currently, their survival appears to be relatively more sensitive to light and herbivory than sycamore and beech at the seedling stage. So, the closure of canopy may be less favourable for ash seedlings.

Sycamore seedlings had a low survival rate when at a small size, but their survival rate increased rapidly with size. So, the number of sycamores could be expected to increase steadily in the long run without major disturbance. It is important to maintain deer management, as survival of ash and beech are both affected by herbivory. The model estimated a 5%-10% omission rate when relocating seedlings. The omission rate could be higher in longer survey and when different surveyors are involved. Mark-recapture method could account for omission and enables us to utilize all existing data to its maximum. Though relatively less frequently used in plant populations, Mark-recapture method can be a suitable tool for analysing survival for juvenile plants which have higher mortality and chances of being overlooked than adult trees.

Chapter 5 Implication of seedling regeneration in forest model and possible changes in forest composition of Wytham Woods

Abstract

Forest models are important tools for predicting forest dynamics in relation to environmental changes and human disturbance. Regeneration at early life-stages is often ignored or simplified in process-based forest models due to a lack of data. By combining collected seedling regeneration data and existing studies, I am able to calibrate a process-based forest model SORTIE, which simulates the whole life cycle of individual trees from seeds to adults in common tree species at Wytham Woods. I run two versions of SORTIE, with and without explicit seedling recruitment, to compare the differences in model prediction and to discuss potential changes in tree distribution over time at Wytham Woods. Both models showed the woods would be dominated by ash and sycamore in 200 years' time, whilst the model with seedling recruitment predicted fewer trees.

Introduction

Forest models are important tools for studying forest succession, the effects of disturbance, management, and climate change (Shugart and Smith 1996, Bugmann 2001, Hartig et al. 2012). They can be used to study forest changes at various spatial and temporal scales, to predict the dynamics of forest species composition, biomass, carbon storage and biodiversity with environment changes. One of the most significant environmental changes of the 21st Century will be climate change, i.e. rising CO_2 (and other greenhouse gases) concentrations, resulting in changing temperature and precipitation. Climate change is likely to have an impact on the performance (growth, survival, fecundity etc.) of individual trees and the properties and functions of forest ecosystems (Kirschbaum 2000, Lindner et al. 2010, Clark et al. 2016). Forest models are particularly valuable for provide insights and advice on managing forest ecosystems and conserving biodiversity with changing climate.

Forest dynamics is the aggregation of a series of biological processes which occur at the individual tree level, such as growth, dispersal, and survival, and result in changes at community and population levels. Individual trees often have strong interactions with their neighbours such as light competition (Canham and Uriarte 2006), which makes it difficult to predict the response of trees at individual level. Thus desirable models for forest dynamic predictions tend to be process-based, which can capture important underlying biological mechanisms and allow changes at higher levels to be an emergent property of the low level processes (Evans et al. 2012, 2013). The development of forest models began in the 1960s and models are diverse in their purpose, complexity, spatial/temporal scale and data needed for parameterization. The earliest models, like JABOWA (Botkin et al. 1972) focused on simulating the dynamics of one or many patches of forests with a number of trees and simulates growth, establishment and mortality processes of these trees, thus named 'gap models' (Bugmann 2001). Early gap models usually do not track individual trees spatial locations due to limitation of computation and model complexity. There were also few interactions between patches. Thus spatially explicit processes like light competition and seed dispersal within and between patches were not explicitly modelled (Van Oijen et al. 2005, Lichstein et al. 2010). Pacala et al. (1996) designed SORTIE, a spatially explicit gap model, which tracks each individual tree's location and is able to simulate light competition between trees providing more realistic simulations than most other gap models (Bugmann 2001). Models like SORTIE treat individual trees as their basic units. The advantage of individual-based models is that many ecological processes are individual-relevant (Grimm 1999). For example, the light received by a tree is the dominant factor on its growth, while the distribution of light is shaped by distribution of individual trees of varying sizes. But individual-based models are usually computationally expensive, and their modelled scales are often less than tens of hectares. Many landscape level forest models, like LANDIS (Mladenoff et al.1993), have been created to study succession and disturbance at larger spatial scales (Mladenoff 2004, Dai et al. 2015). Due to the large spatial scale studied, landscape

forest models usually represent forest in cells characterized by species composition, age class or management type (Taylor et al. 2009)

Parameters of forest gap models are often estimated from observations of simulated ecological processes. A more mechanistic and detailed approach to improve forest models is to incorporate physiological processes. Physiological models are based on modelling the basic physiological processes of trees. These models simulate fundamental physiological processes like photosynthesis, respiration, carbon and nutrient allocation, and water use (Reynolds et al. 2001). This high level of detail makes physiological models desirable options to predict the direct effects of climate change on trees, including, for example, changes in atmospheric CO_2 levels and water availability. There have been many attempts to introduce physiological processes into forest gap models (Friend et al. 1993, Keane et al. 1996). Bugmann (1996) developed ForClim, a model influenced by the carbon and nitrogen cycles to study the dynamic of forest structure in the Alps. However, describing physiological process requires estimation of a large number of parameters, so the structure of physiological models is usually more complex than that of standard gap models. Knowledge of many physiological processes is poor for most species and extremely difficult to measure, which pose difficulties in the application of a physiological model on a new site and with a new species (Bugmann 2001). Moorcroft et al. (2001) developed the ecosystem demography model (ED), which couples individual based gap model to biochemical model describing cycle of carbon, water and nitrogen and scales the result to larger scale. On global scale, DGVMs link physiological processes of plants to ecosystem dynamic and atmospheric CO_2, enabling study of interaction between biosphere and atmosphere (Cramer et al. 2001, Moorcroft 2006).

A major problem of applying process-based forest models, especially spatial-explicit and individual-based ones like SORTIE is the huge data demand needed to parameterize the model. To fully parameterize a model, extensive field measurements are often needed to gather the required data. Long-term monitoring research projects, like the UK Environment Change Network, ForestGEO global network, and forest inventory data can all provide

valuable information to calibrate parameter-heavy forest models. However there are still large gaps between the data collected and the model requirements (Evans and Moustakas 2016). Many existing datasets only record DBH, height growth and mortality of adult and sapling trees, while ignoring seedlings or providing only simple count data. The lack of knowledge of seedling stages is also reflected in the design of forest models. Many early forest gap models assume unlimited seed availability and uniform seed distribution, or do not include explicit seed production, dispersal and seedling establishment processes. Instead all these variables are treated as an aggregated process by introducing saplings directly into the model (Price et al. 2001). However seedling regeneration processes are important for forest succession and should be considered to provide realistic predictions (Ribbens et al. 1994, Clark et al. 1998b, Price et al. 2001).

In this chapter I used the model SORTIE with seed dispersal, seedling growth and mortality processes calibrated as described in previous chapters to explore possible changes in forest composition of Wytham Woods. As already outlined, SORTIE is spatially explicit, with detailed, realistic processes at the individual tree level. It balances sufficient detail against the volume of data needed to calibrate the model. SORTIE was developed for Northern American forests, and has been applied in Europe and New Zealand to study forest succession, effects of climate change, and implications for management (Pacala et al. 1996, Kunstler et al. 2009, Vanhellemont et al. 2011, Ameztegui et al. 2015). The processes influencing sapling and adult tree growth and survival in SORTIE have been calibrated for Wytham Woods in previous work and used to explore the effect of growing season changes and drought frequency changes on forest composition (Carey 2015, Moustakas and Evans 2015). But these works lack seedling establishment data. This means that the former version of SORTIE treats saplings as new recruits and ignores seedlings. To explore the effect of explicitly modelled seedling establishment on predictions, I ran two versions of the models on a simulated forest like Wytham Woods, these being with and without seedling dispersal, growth and survival.

This chapter compared the results, and discussed the potential changes in Wytham Woods based on model outputs.

Method

Brief introduction of SORTIE and previous work

SORTIE simulates the life history of individual trees to model the dynamics of forest communities. In SORTIE each tree species is classified into three age classes: seedling (height <1.35m), sapling (height ≥1.35m and DBH <0.1m) and adult (height ≥1.35m and DBH ≥0.1m). SORTIE consists of several sub-models: resource, growth, recruitment and mortality. The SORTIE version used here is based on Bithell & Brasington (2009). In addition to data collected in this work, existing data of sapling and adult stages of the studied species at Wytham Woods were used to parametrize the model (Carey 2015, Evans et al. 2015, Moustakas and Evans 2015).

Resource sub-model

The central resource which controls individual tree growth in SORTIE is light. The model treats sky as a hemispheric grid and simulates the sun's trajectory over the growing season to calculate the amount of light coming from each cell of the sky.

Each adult or sapling tree has its crown. The size of crown is calculated using allometric equations that relate crown radius and depth to DBH. The attenuation of light passing through the crown is calculated with species-specific light extinction coefficients. When calculating the light received by a tree, the model searches neighbouring trees within a certain radius of the focal tree and calculates the light interception effect of their crowns. The average light availability received by an individual tree in a year is calculated from the spatial and temporal movement of sun and the shading of neighbouring trees. The calculation details can be found in the website of SORTIE (http://www.sortie-nd.org)

Growth sub-model

The annual radial growth of individual tree is calculated with their DBH and the light intensity received with different equation for sapling and adult. The annual radial growth of saplings ($G_{sap,}$ mm/year) is calculated with a Michaelis-Menten function:

$$G_{sap} = \alpha L (L + \alpha/\beta)^{-1} D_{10}^{\varphi} \quad \textbf{equation 5.1}$$

Where:

L is light intensity (% of full light)

D_{10} is diameter at 100mm

α is growth rate in 100% light

β is growth rate in 0% light

φ is parameter controls the size effect

The annual radial growth of adults ($G_{adult, mm/year}$) is calculated with the simplified Neighbourhood Competition Index (NCI) growth equation:

$$G_{adult} = \text{Max G} \times SE \quad \textbf{equation 5.2}$$

Where:

Max G (mm /year) is the maximum growth rate data recorded for the calculated species

SE is a size effect calculated by:

$$SE = e^{-0.5 (\ln(DBH/X_0)/X_b)^2} \quad \textbf{equation 5.3}$$

Where:

X_0 and X_b parameters are estimated from the datasets.

Mortality sub-model

The mortality of trees is modelled with DBH and mean monthly summer rainfall, which are found to be important for tree survival at Wytham Woods with existing data (Evans, Moustakas and Carey, in press). The future rainfall data between 2020-2090 was generated with the Weather Generator on the UK climate projections website (http://ukclimateprojections.metoffice.gov.uk). The survival probabilities for ash and sycamore were calculated as:

$$p = \frac{e^{(\beta_1+\beta_2(\frac{DBH-meanDBH}{sdDBH})+\beta_3 R_{\overline{sm}})}}{e^{(\beta_1+\beta_2(\frac{DBH-meanDBH}{sdDBH})+\beta_3 R_{\overline{sm}})}}$$ **equation 5.4**

Where:

meanDBH and sdDBH are species-specific mean and standard deviation of DBH from existing datasets of trees at Wytham Woods.

$R_{\overline{sm}}$ is the mean monthly summer precipitation.

The survival of beech is not affected by rainfall as the analysis shows reliable parameters could not be obtained (M.R. Evans unpublished).

Recruitment sub-model

The previously parameterized model treats saplings as new recruits because of lack of data on seeds production and dispersal (Carey 2015). The density of saplings (numbers/m^2) at point i R_i is:

$$R_i = STR \sum_{j=1}^{n} ((DBH_j/30)^{\beta} e^{-0.5(\ln(d_{ij}/X_0)/X_b)^2})$$ **equation 5.5**

Where:

STR is the species-specific standardised number of recruits produced by a tree of 300mm DBH

DBH_j is the DBH of the jth tree

d_{ij} is the distance between tree j and point i

x_0, x_b and β are parameters

Since the recruitment parameters for studied species are not available in existing datasets. The parameters were taken from species of the same genus in Northern America from Swift (2005).

Incorporation of seedling recruitment processes

To improve the current model, the seedling growth, allometry, survival, seed production and dispersal results from previous chapters were incorporated into SORTIE.

The growth function was the logistic function for all three species from chapter 3 (equation 3.2):

$g = a/(1 + e^{(b-cl)})$ **equation 5.6**

Where

l is the light intensity and *g* is the relative growth rate

a, *b* and *c* are model parameters (values from Table 3.2)

The survival function varies for different species (Table 5.1). As SORTIE cannot currently include the effects of herbivory for ash and beech, I used the best survival models without herbivory, which are constant survival models:

$p = \frac{e^{\beta}1}{1-e^{\beta}1}$ **equation 5.7**

Where:

p is survival probability of seedling

β is the intercept

For sycamore, the best survival model with effect of seedling size was used:

$$p = \frac{e^{(\beta_1+\beta_2 size)}}{1-e^{(\beta_1+\beta_2 size)}}$$ **equation 5.8**

Where:

β_1 is the intercept

β_2 is the slope of seedling size

As SORTIE currently cannot model the effects of neighbouring environment on seed production and dispersal, the effect is not considered. I used model averaged parameters from chapter 2, Table 2.4 (Table 5.2).

$$S = b * \text{basal area} * exp\left[-\frac{\left(ln\, r - ln\, u - {}^{p}/_{2}{}^{2}\right)^{2}}{2p^{2}}\right] \Big/ (2\pi)^{3/2} pr^{2}$$ **equation 5.9**

Where

S is the number of seeds per square meter

b is fecundity of a tree

r is the distance from source tree to current location

u and p are dispersal parameters

The modelled species were ash, beech and sycamore as they have the most complete data sets. However, germination data for these species is missing. Previous field observations showed germination can range from 10% to 30% for ash (Tapper 1992b) and 50% for sycamore (Jones 1945). In SORTIE, new seedlings appear with a height of 100mm. So seedling establishment in SORTIE is a combination of germination and seedlings reaching a height of 100mm. Seedlings in the first year are prone to high mortality (Tapper 1992b), so the probability of a seedling reaching a height of 100mm should be much lower than the germination rate. Since there is a lack of data and large number of seedlings greatly increases

computation burden, I set the probability of a seed to become a seedling at 1%, for all three species, to eliminate the effect of this unknown process in predictions. From field observations, this rate is probably not too far from reality and makes computation feasible.

To compare the differences between the older model with sapling recruitment (the 'sapling model' hereafter) and the model with seedling recruitment (the 'seedling model' hereafter) in predicting future species composition of Wytham Woods, I ran the two models with similar starting conditions for 200 years, which is close to expected life span for studied species (150-300 years) , with 5 runs for each model. The starting tree composition were set so as to be a realistic sample of Wytham Woods (Table 5.3). The modelled plot is 200m x 200m square with initial trees spreading over the plot (Fig. 5.1).

Table 5.1. Parameters of survival function used in SORTIE for equation 5.7 and 5.8

Species	β_0	β_1
Ash	1.49	/
Beech	1.13	/
Sycamore	-2.64	1.03

Table 5.2. Parameters of seed production and dispersal kernel used in SORTIE for equation 5.9 (From Table 2.4)

Species	b	u	p
Ash	13.1	3.9	-1.2
Beech	10.27	2.71	-2.3
Sycamore	11.5	3.61	-1.96

Table 5.3. Starting tree composition

Species	Age Class	Number	Proportion
Ash	Adult	113	22.4%
Ash	Sapling	61	12.2%
Sycamore	Adult	205	40%
Sycamore	Sapling	94	18.8%
Beech	Adult	6	1.2%
Beech	Sapling	26	5.2%

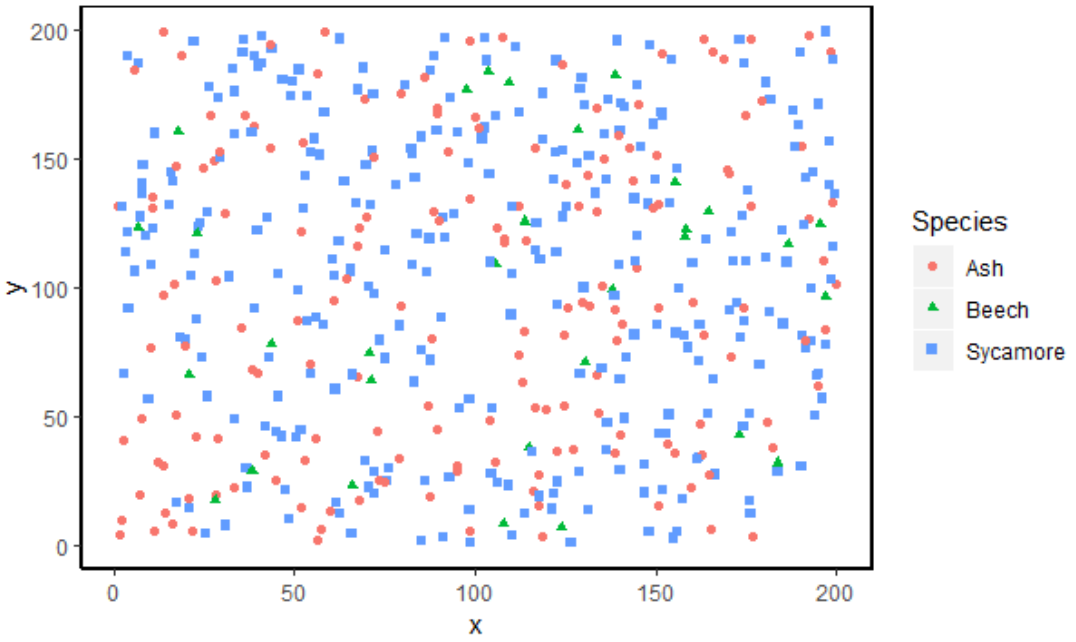

Fig.5.1. Starting tree distribution

Differences in species-specific proportion representations between model predictions and starting composition were compared with a t test for each type of model. Differences in averaged number, proportions of trees and DBH were tested by a two-way ANOVA with species and model type as group factors, for adult and sapling age class separately. Seedling number and proportion were compared between species for the seedling model with a one-way ANOVA. A Tukey HSD test was used to perform pair-wise comparisons when significant difference was found between groups. The spatial distributions of trees at the end of the runs for the two models were also compared.

Results

Species Composition

Compared to the starting conditions, both the sapling and seedling model predicted significantly increased proportions of ash and beech after 200 simulated years, while proportions of sycamore significantly decreased. In the output of the sapling model, the average proportion of ash and beech increased from 34.6% to 44.6% and 6.4% to 9% respectively (t test, $p<0.01$ for both). While sycamore decreased to 46% from starting 59% (t test, $p<0.01$). In the seedling model, ash and beech proportion increased to 43.4% (t test, $p=0.02$) and 10% (t test, $p=0.02$), while sycamore proportion decreased to 45.6% (t test, $p<0.01$).

ANOVA showed there were significant differences in both the number of adults and proportions of the different tree species ($p<0.01$), as well as differences in number of adults between models ($p<0.01$, $F_{1,30}=29.11$). The sapling model predicted more adult trees than the seedling model for all species (Fig 5.2). Both sycamore and ash have significantly higher numbers and percentage than beech (Tukey HSD test, Fig. 5.2. and 5.3.). Sycamore also had higher number and percentage than ash.

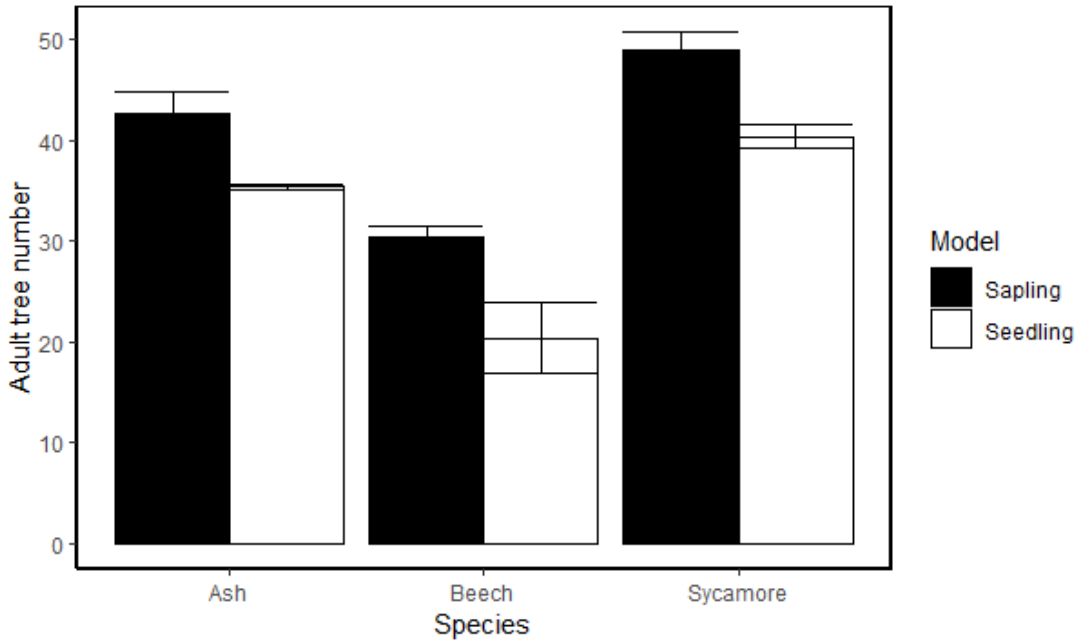

Fig.5.2. Averaged absolute adult tree number from seedling and sapling models after 200 simulated years

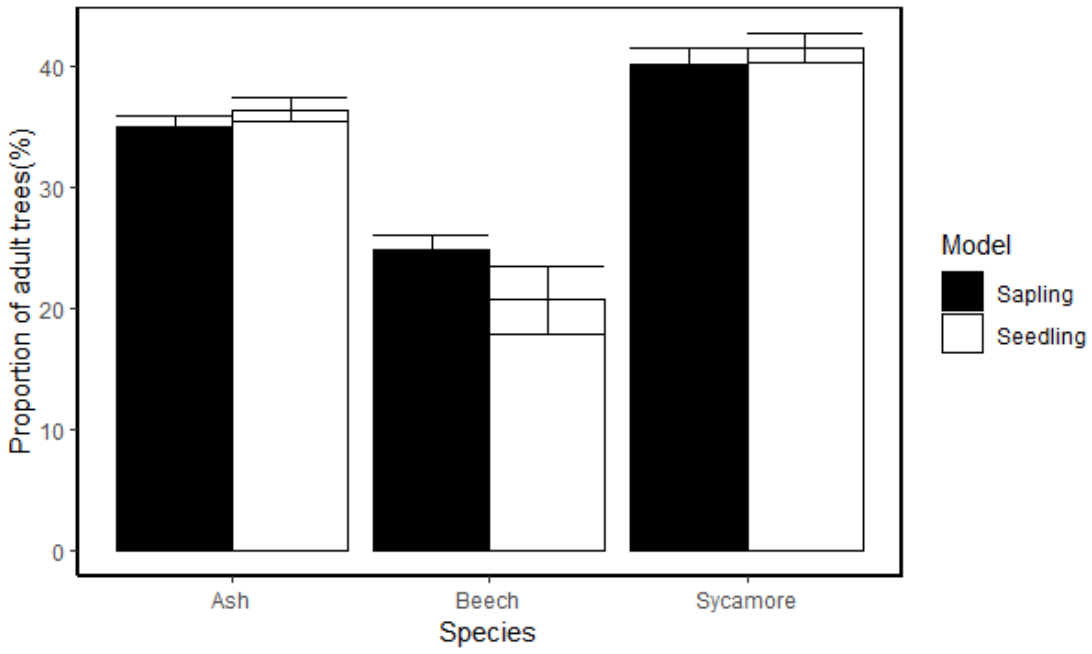

Fig.5.3. Averaged adult tree proportions from seedling and sapling models after 200 simulated years

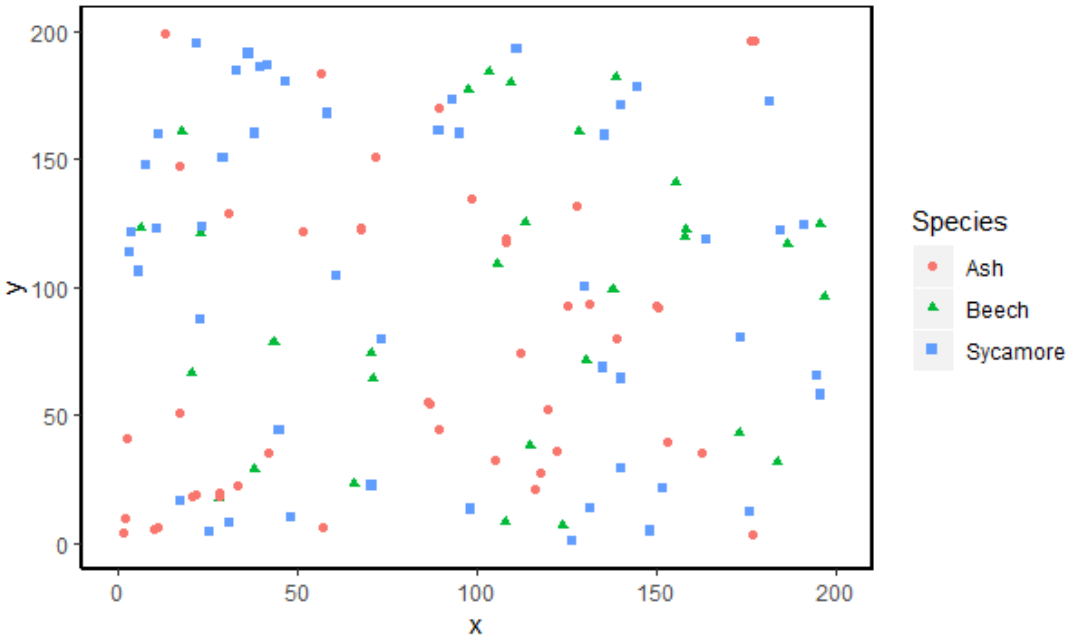

Fig 5.4 Predicted adult tree distribution at the end of a sapling model run after 200 simulated years Sapling model predicted more adult trees than seedling model (Fig 5.5)

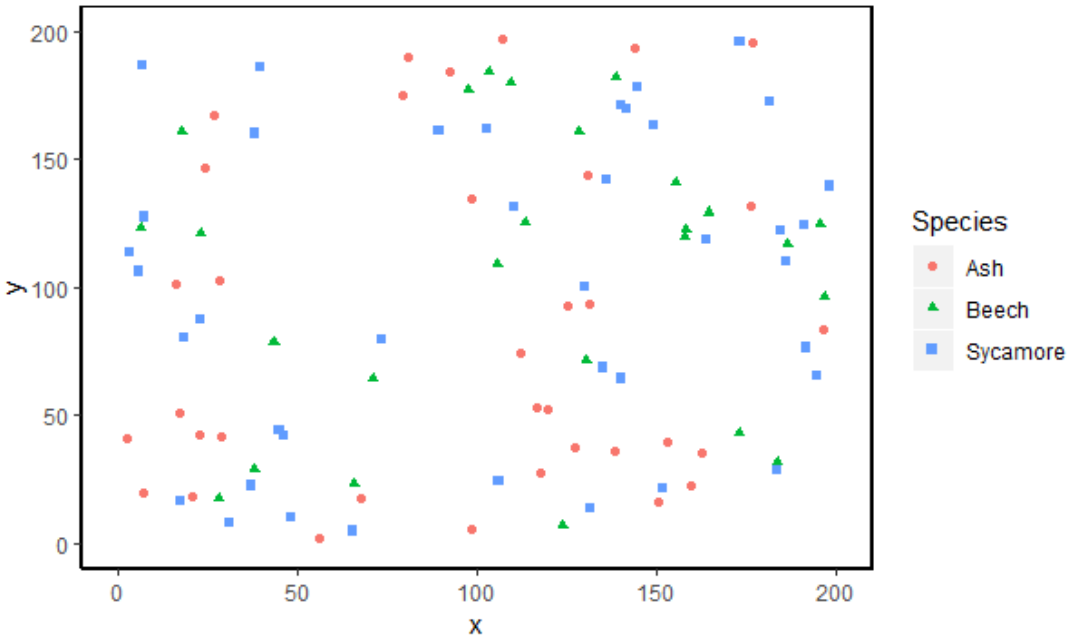

Fig 5.5 Predicted adult tree distribution at end of a seedling model run after 200 simulated years

Significant differences also existed in the number of saplings between different species (ANOVA, $F_{2,30}$=383.2, p<0.01) and models (seedling and sampling models, ANOVA, $F_{1,30}$=843.2, p<0.01). The sapling model predicted more saplings than the seedling model for all species. Sycamore also had significantly more saplings than beech predicted by both models (Tukey HSD test, Fig.5.6.). The proportion of saplings differs significantly between species (ANOVA, $F_{2,30}$=559.56, p<0.01) but not between models (ANOVA, $F_{1,30}$=145.9, p=0.1). Tukey HSD test showed that both sycamore and ash had significantly higher proportions of saplings than beech but not significantly different from each other (p<0.05) in the output of the both models (Fig 5.7).

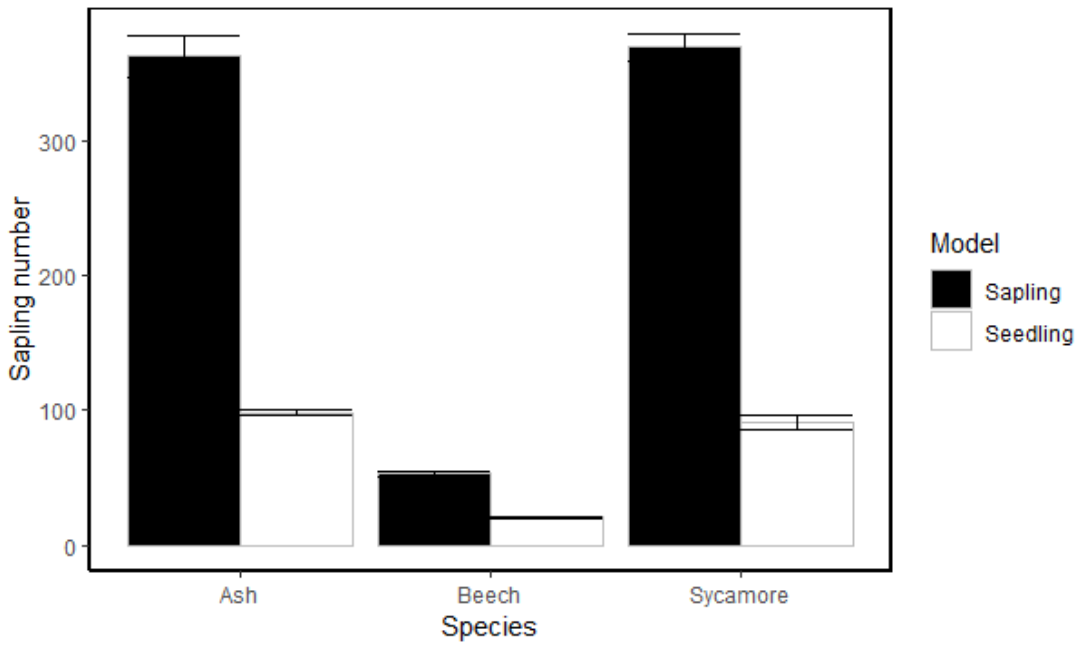

Fig.5.6. Averaged sapling numbers in seeding and sapling models after 200 simulated years

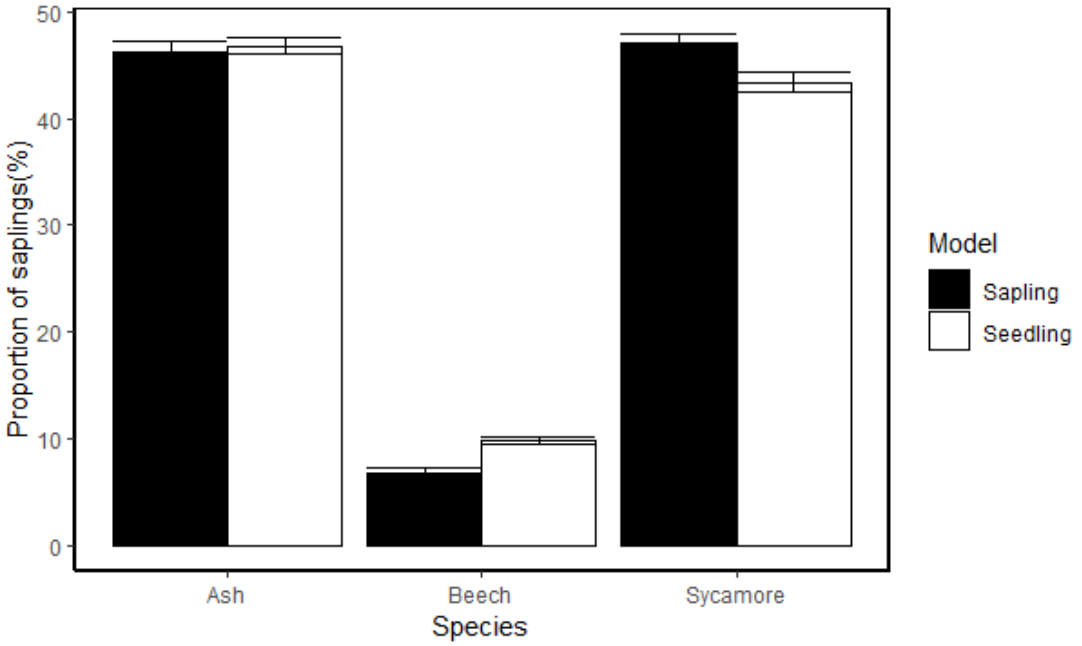

Fig.5.7. Averaged sapling proportions in seeding and sapling models after 200 simulated years

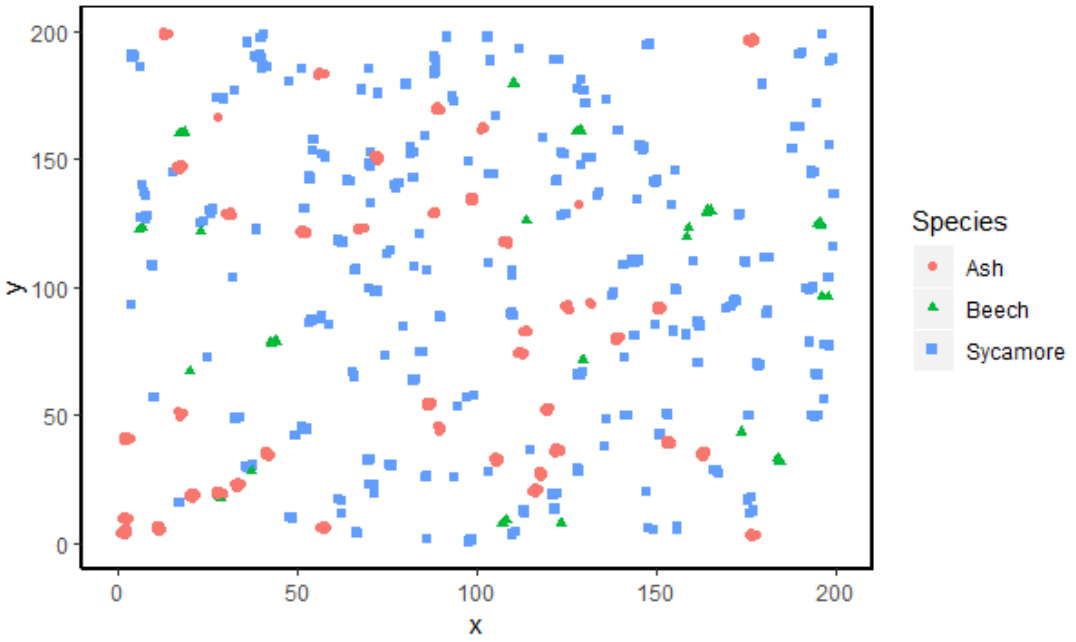

Fig 5.8 Predicted sapling distribution after a sapling model run after 200 simulated years The sapling model predicted more saplings than the seedling model (Fig 5.9)

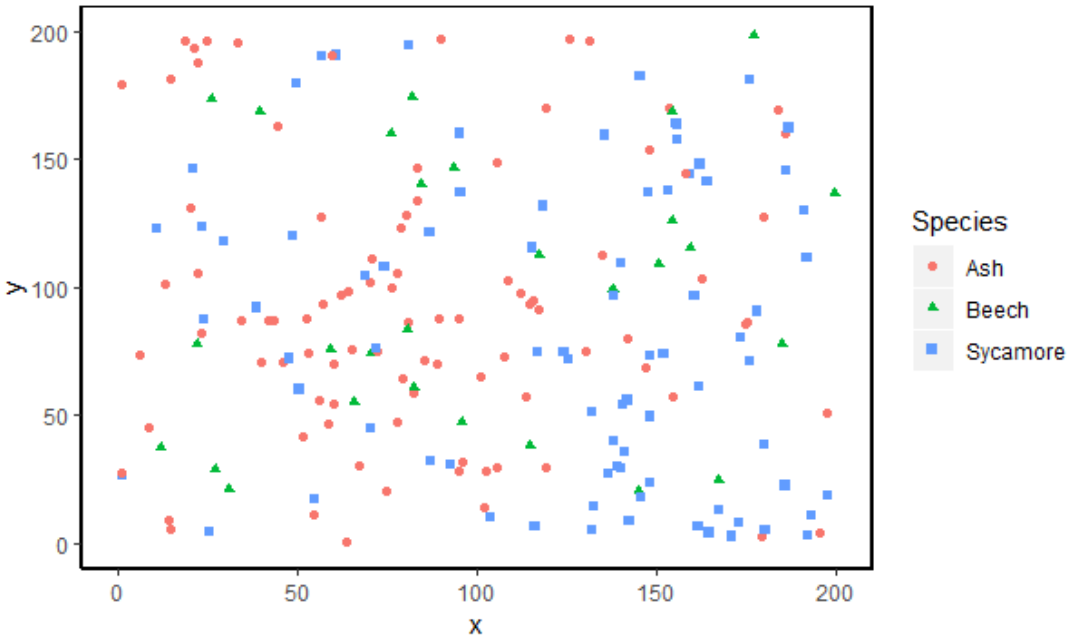

Fig 5.9 Predicted sapling distribution after a seedling model run after 200 simulated years

In seedling composition, ash was the most abundant with on average 80% of seedlings being ash, significantly higher than both sycamore and beech (Tukey HSD test, $p<0.05$, Fig.5.10. and Fig.5.11).

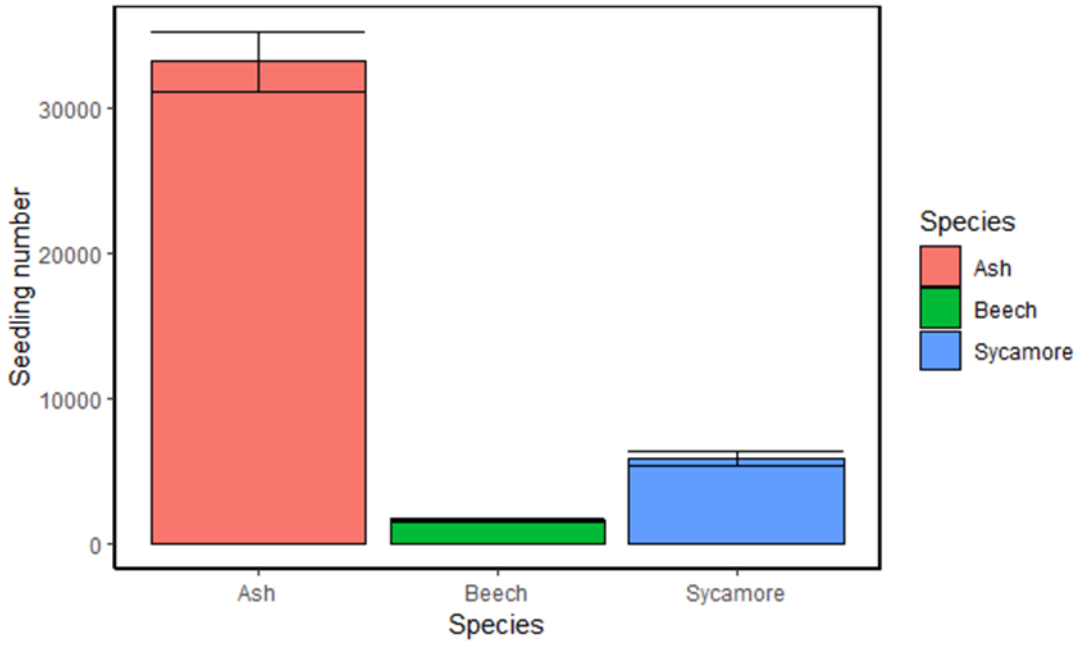

Fig.5.10. Averaged seedling number of different species predicted by the seedling model after 200 simulated years

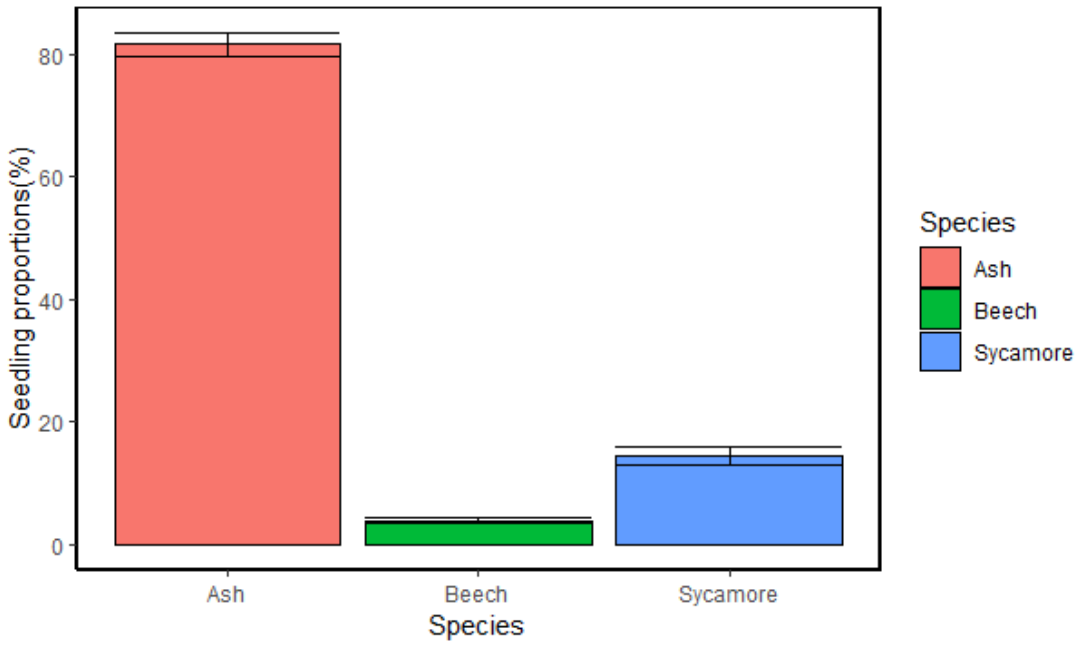

Fig.5.11. Averaged seedling proportions of different species predicted by the seedling model after 200 simulated years

Tree Size Distribution

There were significant differences in average basal area across both species (ANOVA, $F_{2,30}$=697.86, p<0.01) and models (ANOVA, $F_{1,30}$=170.24, p<0.01, Fig 5.12). Within both models, beech had higher average basal area than ash and sycamore, and ash also had significantly higher average basal area than sycamore (Tukey HSD test). Mean basal area of three species were significantly lower in predictions of sapling models (Fig 5.12).

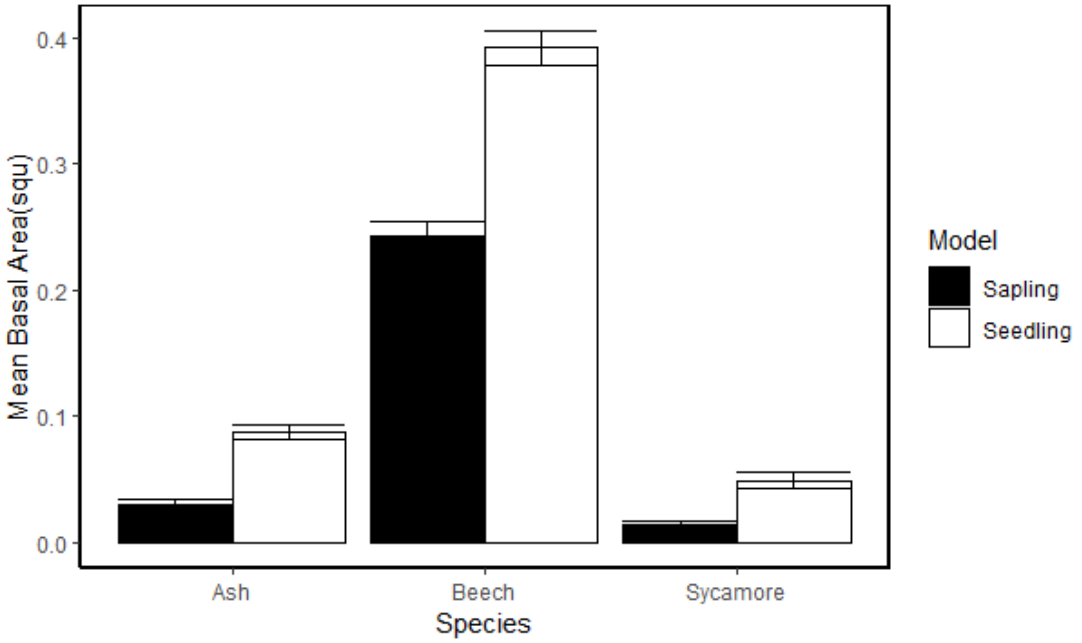

Fig.5.12. Mean basal area of tree species predicted by different sapling and seedling models after 200 simulated years

Discussion

After running the models for 200 simulated years, the species composition and tree number of both models showed some significant changes from the initial condition and significant differences to each other. This shows that the incorporation of seedling recruitment processes had impacted the modelled forest dynamics. However, both models predicted similar general trend in forest dynamic: that the percentage of sycamore decreased, whilst both ash and beech increased.

The sapling model produced more adult trees and saplings than the seedling model. This is because the sapling model produced saplings directly while seedling model introduced new recruits as seedlings. As the modelled plot is under closed canopy with average light intensity of 30%, it would take years for a seedling to grow into a sapling. The sapling model could have overestimated the number of adult and sapling trees. The sapling model also produced lower average basal area because of lower adult to sapling ratio.

Though two models predicted contrasting number of trees, the composition of species is similar. Sycamore remained the most abundant species, but its percentage was reduced compared to starting condition, with ash and beech rising in species composition. Beech increased in proportion but still remained relatively rare. Ash had also become more prevalent because in both model ash had higher fecundity than sycamore and beech. In the seedling population predicted by the seedling model, ash was the most dominant, with more seedlings than the sum of other two species. This is in line with previous surveys on seedling abundance (Kirby et al. 2014). The large size of the ash seedling reservoir can facilitate dominance of ash. If future disturbance creates new open areas in the forest, ash seedlings would be able to take greatest advantage because seedlings were likely to be present. The two models both predicted that the forest will still be co-dominated by ash and sycamore after 200 years with sycamore decreasing in percentage, which is in agreement with a study suggesting ash will out compete sycamore to become the most dominant species in the future at Wytham Woods (Morecroft et al. 2008).

There are some important factors not considered in these simulations. For example, the three modelled species have different optimal soil types for growth (Packham and Thomas 2012, Thomas 2016). The seedling model generates new seedling start at 100mm height. However small seedlings have high mortality are most prone to density-dependent mortality caused by pathogens or predators, which may have different effects on the studied species. Ash and sycamore with high seedling densities could suffer more than beech. More data on smaller seedlings needs to be collected to provide information if this is a concern. The studied species

are known for highly variable seed production (Tapper 1992a, Hilton and Packham 2003). The variation in seed production can have a substantial impact on species composition, which cannot be modelled by current model. However the predicted results were in general consistent with observed trends in forest dynamics at Wytham Woods (Kirby et al. 2014). Sycamore and ash would remain co-dominant in the community, where sycamore have larger number of sapling and adult trees, but ash trees are more prevalent in seedling community and would increase gradually.

Sycamore is thought to be less tolerant to drought than ash. Thus, predicted increasing drought frequencies would lead to sycamore decrease (Carey 2015). An important factor to be incorporated is the occurrence of ash dieback. Ash dieback is an emerging disease causing losses of ash trees, including entire populations in Europe. This disease has also been found in the UK recently (Pautasso et al. 2013, Mitchell et al. 2014). Though this disease has not yet reached Wytham Woods, it poses a great threat to forest biodiversity conservation and management. The outbreak of ash dieback is predicted to have a large impact on ash populations and the loss of ash would lead to the rise of sycamore and other canopy trees in population size (Needham et al. 2016). As ash dieback affects all life stages of ash, it would also have a large effect on seedling regeneration. (Gross et al. 2014)

Chapter 6 General Discussion

In this thesis I have examined several processes that are critical to tree regeneration in temperate European forests. I then relate these processes to environmental conditions to increase understanding of forest dynamics. Forest regeneration is the combined outcome of various processes including seed production, dispersal and seedling establishment which need to be modelled explicitly, so that we can better predict how forests will respond to environmental change. All too often, when modelling forest changes, regeneration processes are aggregated and simplified, due to limited data availability (Busing and Mailly 2004). But with suitable, enhanced data sets, as obtained in this thesis, coupled with high-performance computing, we can increase our understanding of forest dynamics, and improve process-based forest models.

I investigated here seed production and dispersal with the Inversing Modelling (IM) approach and showed that the neighbouring environment can affect both tree fecundity and seed dispersal. There are relatively few studies utilizing IM to study seed dispersal of trees in Europe. The estimated dispersal distances of seeds at Wytham Woods are higher but similar in scale to Clark et al. (1998b) in Northern America, who estimated mean dispersal distance for wind-dispersed trees ranged from 19 to 37 m. This compares with 25 to 66 m at Wytham Woods. My result showed, at Wytham Woods, both fecundity and the shape of seed dispersal kernel of the studied species changed between years, which is also consistent with a study on dispersal kernels of five tree species in Spain (Martínez and González-Taboada 2009), who estimated median dispersal distance of beech ranged from 6.7 to 169 m between years. Varying dispersal kernel shapes suggest for both wind and animal-dispersed species at Wytham Woods, that dispersal processes can be affected by various environmental conditions. Variations in wind conditions can also lead to changes in dispersal kernels of wind-dispersed species. For animal-dispersed species, the crop produced by trees can affect the behaviour of animal dispersers. As a result, a fixed dispersal kernel without considering

various factors will perform poorly when predicting dispersal patterns into the future. Moreover, the incorporation of environment factors (neighbouring tree density) improved the performance of models, as has been found in other studies that applied this approach (Schurr et al. 2008, Herrera et al. 2011), but the effect was also not consistent between years. The result presented here have enhanced the long-standing opinion that seed dispersal is a complex ecological process. Thus, it is desirable to identify and incorporate more ecological factors into seed dispersal modelling. The high temporal variation in seed production makes estimating fecundity from tree size alone sub-optimal (Clark et al. 2004).

Seed production is largely the result of resource allocation by trees, so a better understanding of resource uptake and allocation may also enable models of seed production to be more accurate (Vacchiano et al. 2018). The fecundity of a tree in any particular year may be affected by its resource allocation to seeds in previous years. For example, a tree may accumulate and store resources over several years to produce a high seed crop in subsequent years, and increased allocations to seed production may reduce growth rates (Koenig et al. 1994, Sala et al. 2012). As a consequence, incorporating previous fecundity and growth rate of individual trees may improve the performance of models (Ogle et al. 2015).

Here too I studied growth and survival of seedlings, on which quantitative data are few for the studied species (Petritan et al. 2007). As expected, light is an important factor influencing seedling growth, which is consistent with a study on sapling stages of the studied species (Stancioiu and O'Hara 2006, Petritan et al. 2009). However, the results here do not show any obvious trade-off between high-light growth rate and low-light survival, as reported in many other studies. This may be because the studied species are shade-tolerant and partitioning the light niche is unlikely to be the main factor of their coexistence. The studied species did not present large differences in growth rates across light gradients, reflecting their similarity as shade-tolerant species. But the result on seedling survival is more complicated, with only the survival of ash seedlings being best explained by a model that contained the effect of light. The results could be attributed to the limited sample size of seedlings from low light

availability (<20%) environment. Saplings of studied species have been found approaching zero mortality just above 15% light availability (Petritan et al. 2007).

The effect of herbivory was found to be important in explaining the survival of both ash and beech. The result of the survival study, combined with high prevalence of browsing signs in sampled seedlings, suggests herbivory plays an important role in the dynamics of seedling recruitment at Wytham Woods. An effect of herbivory on growth rate was not found at Wytham Woods, which was probably due to the very simple measurement of herbivory applied. A more detailed study aiming at the effect of herbivory is needed to explore if browsing does influence growth and how the timing and intensity of browsing affect seedlings. The differences between my results on tree seedlings and previous studies on saplings could also be due to local site differences (soils, climate, herbivores presence), as well as to differing responses to environmental conditions at different life stages of juvenile trees.

Another potential important biological factor affecting seedling performance is distance to, and frequency of, conspecific adults. Waters and Savill (1992) found ash and sycamore seedlings regenerated better under the canopy of the other species rather than their own, a pattern which is likely to be caused by distance-dependent herbivory or pathogen attack. A study has shown negative distance-dependent effect in mortality of sycamore seedlings driven by higher herbivory of invertebrate predators near conspecific adults (Pigot and Leather 2008). The negative distance-dependent effect on seeding survival could have contributed to increase of ash in Wytham Woods and other forests across the UK (Mihok et al. 2009) and is likely to lead to alternation of dominance in the future.

With seedling production, dispersal, growth and survival processes calibrated from field data, I used an individual-based forest model to explore the difference between models with, and without, explicit seedling recruitment. The result showed that incorporating seedling regeneration could lead to significant differences in the proportions of each species and in contrasting spatial structures. Nevertheless, the model still predicts 200 years into the future

and suggests a co-dominance of ash and sycamore, as currently occurs, but with an increased proportion of ash. Beech would still be a minor component of the woods due to low adult abundances, fecundity and short dispersal distances. This result is consistent with observed past trends in the woods (Mihok et al. 2009), but it does not consider potential catastrophic processes, such as ash-die back disease Some tree species with high ecological value, like oak and field maple, could not be included in this study because of the scarcity of seedlings. That scarcity is consistent with previous surveys (Kirby et al. 2014), and may indicate failure of regeneration in these species, the reason for which needs further study. But introduction of a distance-dependent effect such as that discussed above may lead to interesting results. The responses of seedlings to climate change and the potential emergence of ash dieback are likely to have important effects on forest species composition and are worthy of further studies.

In this thesis, I studied important stages in seedling regeneration, which has received less attention in existing forest monitoring projects than adult stages. The collection of field data regarding seedling regeneration is time consuming but important. The scarcity of knowledge on seedling regeneration often poses problems when building process-based predictive forest models (Busing and Mailly 2004, Evans and Moustakas 2016). I modelled seed production and dispersal kernel for four common tree species. To my knowledge, no study on these species, except beech, has been done before using the inversing modelling approach ((Martínez and González-Taboada 2009). Thus, this study filled the gap of knowledge on dispersal of studied species. The knowledge of seed production and dispersal will enable better prediction of regeneration and distribution changes of studied species, and will likely to be relevant to woodlands that are dominated by these species. The result showed significant annual variation of seed production as well as effect of surrounding environment on seed dispersal. Currently most forest models employ a fixed dispersal kernel, and simulation of temporal variation in fecundity is often missing (Vacchiano et al. 2018). In future, I suggest that incorporation of temporal variation and effect of external environment is an important

task for modelling of seed production and dispersal. I also modelled seedling growth and survival with important environmental factors like light and herbivory. The results revealed species-specific responses of seedlings to limiting external factors, increasing understanding of early life stage of studied species. The results provided basic yet important knowledge of tree regeneration in an English forest, which are fundamental for forest models like SORTIE to simulate future changes of forest. I didn't test if explicitly incorporation of early life stages can bring more accurate prediction of forest dynamic. However, a simple comparison of models with and without seedling regeneration processes produced different results in case of tree number, age and size distribution, highlighting impact of seedling regeneration on model output. More work can be done on basis of these results to test to how much details and realism are needed to further refine models for accurate prediction by forest models.

The study has a short time span and limited sample size. A longer study could have led to better understanding of forest regeneration at Wytham Woods. There was large variation in seed production between years, and factors underlying this variation are not captured by current models. Seed production is a complex process and the mechanism leading to seed production variation is not fully clear (Vacchiano et al. 2018). Longer and larger-scale study can bring more knowledge of seed production pattern. Long-time metrological data can also be used in modelling of seed dispersal. I used inversed modelling, which is a statistical approach of modelling seed production and dispersal. As discussed in chapter 2, a mechanistic model which captures the underlying process may better model the variation in seed production and dispersal. The results of seedling growth and survival part also should be interpreted with caution due to limited sample size that was feasible to study in this work. The result didn't show significant effect of herbivory on seedling growth but herbivory was important for seedling survival. I recommend that the effect of herbivory on seedling at Wytham Woods is worthy of further investigation into the future.

The results here are likely to have wider applications to temperate forests into the future. Wytham Woods is an ancient woodland, which once dominated much of the ecology of

Britain and Northern Europe. Now, through human pressure its scale is reduced to fragmented, isolated populations which need to be carefully managed if it is to survive in the long term, especially in the face of climate change, where range expansion and range movement is restricted. That management needs to be well informed by science-based knowledge of forest dynamics, as is being attempted here through incorporating to models the dynamics of seed dispersal and seedling recruitment.

References

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. (Ted) Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J.-H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* **259**:660–684.

Ameztegui, A., L. Coll, and C. Messier. 2015. Modelling the effect of climate-induced changes in recruitment and juvenile growth on mixed-forest dynamicss: The case of montane–subalpine Pyrenean ecotone. *Ecological Modelling* **313**:84–93.

Araújo, M. B., D. Alagador, M. Cabeza, D. Nogués-Bravo, and W. Thuiller. 2011. Climate change threatens European conservation areas. *Ecology Letters* **14**:484–492.

Araújo, M. B., and A. Guisan. 2006. Five (or so) challenges for species distribution modelling. *Journal of Biogeography* **33**:1677–1688.

Astrup, R., K. D. Coates, and E. Hall. 2008. Recruitment limitation in forests: Lessons from an unprecedented mountain pine beetle epidemic. *Forest Ecology and Management* **256**:1743–1750.

Atkinson, M. D. 1992. *Betula Pendula* Roth (*B. Verrucosa* Ehrh.) and *B. Pubescens* Ehrh. *The Journal of Ecology* **80**:837.

Baraloto, C., D. E. Goldberg, and D. Bonal. 2005. Performance trade-offs among tropical tree seedlings in contrasting microhabitats. *Ecology* **86**:2461–2472.

Bazzaz, F. A. 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* **10**:351–371.

Beckage, B., and J. S. Clark. 2003. Seedling survival and growth of three forest tree species:

The role of spatial heterogeneity. *Ecology* **84**:1849–1861.

Beckage, B., B. Osborne, D. G. Gavin, C. Pucko, T. Siccama, and T. Perkins. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences of the United States of America* **105**:4197–4202.

Berkowitz, A. R., C. D. Canham, and V. R. Kelly. 1995. Competition vs. Facilitation of Tree Seedling Growth and Survival in Early Successional Communities. *Ecology* **76**:1156–1168.

Bloor, J. M. G., and P. J. Grubb. 2003. Growth and mortality in high and low light: trends among 15 shade-tolerant tropical rain forest tree species. *Journal of Ecology* **91**:77–85.

Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. *The Journal of Ecology* **60**:849.

Brasier, C. M. 1979. Dual origin of recent Dutch elm disease outbreaks in Europe. *Nature* **281**:78–80.

Briggs, J. S., S. B. Vander Wall, and S. H. Jenkins. 2009. Forest rodents provide directed dispersal of Jeffrey pine seeds. *Ecology* **90**:675–687.

Brokaw, N., and R. T. Busing. 2000. Niche versus chance and tree diversity in forest gaps. *Trends in Ecology & Evolution* **15**:183–188.

Brusca, R. C., J. F. Wiens, W. M. Meyer, J. Eble, K. Franklin, J. T. Overpeck, and W. Moore. 2013. Dramatic response to climate change in the Southwest: Robert Whittaker's 1963 Arizona Mountain plant transect revisited. *Ecology and Evolution* **3**:n/a-n/a.

Bugmann, H. 2001. A review of forest gap models. *Climatic Change* **51**:259–305.

Bullock, J. M., L. Mallada González, R. Tamme, L. Götzenberger, S. M. White, M. Pärtel,

and D. A. P. Hooftman. 2017. A synthesis of empirical plant dispersal kernels. *Journal of Ecology* **105**:6–19.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. A practical information-theoretical approach. *Springer, New York,USA*.

Busing, R., and D. Mailly. 2004. Advances in spatial, individual-based modelling of forest dynamics. *Journal of Vegetation Science* **15**:831–842.

Butt, N., G. Campbell, and Y. Malhi. 2009. Initial results from establishment of a long-term broadleaf monitoring plot at Wytham Woods, Oxford, UK. *University of Oxford, Oxford,UK*.

Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. *American journal of botany* **87**:1217–1227.

Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* **20**:620–631.

Canham, C. D., A. C. Finzi, S. W. Pacala, and D. H. Burbank. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research* **24**:337–349.

Canham, C. D., M. J. Papaik, M. Uriarte, W. H. McWilliams, J. C. Jenkins, and M. J. Twery. 2006. Neighborhood analyses of canopy tree competition along environmental gradients In New England forests. *Ecological Applications* **16**:540–554.

Canham, C. D., and M. Uriarte. 2006. Analysis of neighborhood dynamics of forest ecosystems using likelihood methods and modeling. *Ecological Applications* **16**:62–73.

Carey, G. 2015. Climate change effects on UK woodlands: can species' interactions mitigate

the impacts of increased drought? *Queen Mary University of London*.

Cavin, L., E. P. Mountford, G. F. Peterken, and A. S. Jump. 2013. Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Functional Ecology* **27**:1424–1435.

Chen, I.-C., J. K. Hill, R. Ohlemuller, D. B. Roy, and C. D. Thomas. 2012. Rapid range shifts of species rapid range shifts of species associated with high levels of climate warming. *Science* **1024**:17–20.

Clark, C. J., J. R. Poulsen, D. J. Levey, and C. W. Osenberg. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *The American naturalist* **170**:128–42.

Clark, C., J. Poulsen, and B. Bolker. 2005. Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology* **86**:2684–2694.

Clark, D., and D. Clark. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *American Naturalist*:769–788.

Clark, J., S. LaDeau, and I. Ibanez. 2004. Fecundity of trees and the colonization-competition hypothesis. *Ecological Monographs* **74**:415–442.

Clark, J. S., B. Beckage, P. Camill, B. Cleveland, J. HilleRisLambers, J. Lichter, J. McLachlan, J. Mohan, and P. Wyckoff. 1999a. Interpreting recruitment limitation in forests. *American Journal of Botany* **86**:1–16.

Clark, J. S., C. Fastie, G. Hurtt, S. T. Jackson, C. Johnson, G. A. King, M. Lewis, J. Lynch, S. Pacala, C. Prentice, E. W. Schupp, T. Webb, and P. Wyckoff. 1998a. Reid's Paradox of rapid plant migration. *BioScience* **48**:13–24.

Clark, J. S., L. Iverson, C. W. Woodall, C. D. Allen, D. M. Bell, D. C. Bragg, A. W.

D'Amato, F. W. Davis, M. H. Hersh, I. Ibanez, S. T. Jackson, S. Matthews, N. Pederson, M. Peters, M. W. Schwartz, K. M. Waring, and N. E. Zimmermann. 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Global Change Biology* **22**:2329–2352.

Clark, J. S., E. Macklin, and L. Wood. 1998b. Stage and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs* **68**:213–235.

Clark, J. S., E. Macklin, and L. Wood. 1998c. Stages and spatial scales of recruitment limitation in southern Appalachian forest. *Ecological Monographs* **68**:213–235.

Clark, J., M. Silman, and R. Kern. 1999b. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* **80**:1475–1494.

Clobert, J., M. Baguette, T. Benton, and J. Bullock. 2012. Dispersal Ecology and Evolution. *Oxford University Press*.

Comita, L. S., S. A. Queenborough, S. J. Murphy, J. L. Eck, K. Xu, M. Krishnadas, N. Beckman, Y. Zhu, and L. Gómez-Aparicio. 2014. Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *The Journal of ecology* **102**:845–856.

Coomes, D. A., P. J. Grubb, E. Monographs, and N. May. 2007. Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. *Ecological Monographs* **70**:171–207.

Coomes, D. A., G. Kunstler, C. D. Canham, and E. Wright. 2009. A greater range of shade-tolerance niches in nutrient-rich forests: an explanation for positive richness-productivity relationships? *Journal of Ecology* **97**:705–717.

Corlett, R. T., and D. A. Westcott. 2013. Will plant movements keep up with climate change? *Trends in Ecology & Evolution* **28**:482–488.

Corney, P. M., K. J. Kirby, M. G. Le Duc, S. M. Smart, H. A. McAllister, and R. H. Marrs. 2008. Changes in the field-layer of Wytham Woods - assessment of the impacts of a range of environmental factors controlling change. *Journal of Vegetation Science* **19**:287–298.

Côrtes, M. C., and M. Uriarte. 2013. Integrating frugivory and animal movement: a review of the evidence and implications for scaling seed dispersal. *Biological Reviews* **88**:255–272.

Cramer, W., A. Bondeau, F. I. Woodward, I. C. Prentice, R. A. Betts, V. Brovkin, P. M. Cox, V. Fisher, J. A. Foley, A. D. Friend, C. Kucharik, M. R. Lomas, N. Ramankutty, S. Sitch, B. Smith, A. White, and C. Young-Molling. 2001. Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. *Global Change Biology* **7**:357–373.

Dai, E., Z. Wu, X. Wang, H. Fu, W. Xi, and T. Pan. 2015. Progress and prospect of research on forest landscape model. *Journal of Geographical Sciences* **25**:113–128.

Dalling, J. W., M. D. Swaine, and N. C. Garwood. 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. *Ecology* **79**:564–578.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Biodiversity conservation in a changing climate. *Science* **332**:53–58.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* **18**:431–451.

Dobrowski, S. Z., J. H. Thorne, J. A. Greenberg, H. D. Safford, A. R. Mynsberge, S. M. Crimmins, and A. K. Swanson. 2011. Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. *Ecological Monographs* **81**:241–257.

Doody, C. N., and C. O'Reilly. 2011. Effect of long-phase stratification treatments on seed germination in ash. *Annals of Forest Science* **68**:139–147.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* **40**:677–697.

Ericsson, T., and T. Ingestad. 1988. Nutrition and growth of birch seedlings at varied relative phosphorus addition rates. *Physiologia Plantarum* **72**:227–235.

Evans, M. R., M. Bithell, S. J. Cornell, S. R. X. Dall, S. Díaz, S. Emmott, B. Ernande, V. Grimm, D. J. Hodgson, S. L. Lewis, G. M. Mace, M. Morecroft, A. Moustakas, E. Murphy, T. Newbold, K. J. Norris, O. Petchey, M. Smith, J. M. J. Travis, and T. G. Benton. 2013. Predictive systems ecology. *Proceedings of the Royal Society of London B: Biological Sciences* **280**:20131452.

Evans, M. R., and A. Moustakas. 2016. A comparison between data requirements and availability for calibrating predictive ecological models for lowland UK woodlands: learning new tricks from old trees. *Ecology and Evolution*.

Evans, M. R., A. Moustakas, G. Carey, Y. Malhi, N. Butt, S. Benham, D. Pallett, and S. Schäfer. 2015. Allometry and growth of eight tree taxa in United Kingdom woodlands. *Scientific Data* **2**:150006.

Evans, M. R., K. J. Norris, and T. G. Benton. 2012. Predictive ecology: systems approaches. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **367**:163–169.

Finch-Savage, W. E., and G. Leubner-Metzger. 2006. Seed dormancy and the control of germination. *The New phytologist* **171**:501–23.

Friend, A. D., H. H. Schugart, and S. W. Running. 1993. A physiology-based gap model of

forest dynamics. *Ecology* **74**:792–797.

Gerhardt, P., J. M. Arnold, K. Hackländer, and E. Hochbichler. 2013. Determinants of deer impact in European forests – A systematic literature analysis. *Forest Ecology and Management* **310**:173–186.

Gilbert, G. S., K. E. Harms, D. N. Hamill, and S. P. Hubbell. 2001. Effects of seedling size, El Niño drought, seedling density, and distance to nearest conspecific adult on 6-year survival of Ocotea whitei seedlings in Panamá. *Oecologia* **127**:509–516.

Gill, R. M. A. 1992a. A review of damage by mammals in north temperate forests: 1. deer. 2. small mammals. 3. impact on trees and forests. *Forestry* **65**:145–169.

Gill, R. M. A. 1992b. A Review of Damage by Mammals in North Temperate Forests: 3. Impact on Trees and Forests. *Forestry* **65**:363–388.

Gill, R. M. A., and V. Beardall. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry* **74**:209–218.

Gillespie, R. G., B. G. Baldwin, J. M. Waters, C. I. Fraser, R. Nikula, and G. K. Roderick. 2012. Long-distance dispersal: a framework for hypothesis testing. *Trends in Ecology & Evolution* **27**:47–56.

Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2010. Shade tolerance, canopy gaps and mechanisms of coexistence of forest trees. *Oikos* **119**:475–484.

Gray, A. N., and T. A. Spies. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. *The Journal of Ecology* **84**:635.

Greene, D. F., J. C. Zasada, L. Sirois, D. Kneeshaw, H. Morin, I. Charron, and M.-J. Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree

species. *Canadian Journal of Forest Research* **29**:824–839.

Greene, D., and E. Johnson. 1989. A model of wind dispersal of winged or plumed seeds. *Ecology* **70**:339–347.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling* **115**:129–148.

Gross, A., O. Holdenrieder, M. Pautasso, V. Queloz, and T. N. Sieber. 2014. *Hymenoscyphus pseudoalbidus* , the causal agent of European ash dieback. *Molecular Plant Pathology* **15**:5–21.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* **52**:107–145.

Hampe, A. 2011. Plants on the move: The role of seed dispersal and initial population establishment for climate-driven range expansions. *Acta Oecologica* **37**:666–673.

Hannon, S. J., R. L. Mumme, W. D. Koenig, S. Spon, and F. A. Pitelka. 1987. Poor acorn crop, dominance, and decline in numbers of acorn woodpeckers. *Journal of Animal Ecology* **56**:197–207.

Harmer, R. 1994. Natural regeneration of broadleaved trees in Britain: Ii seed production and predation. *Forestry* **67**:275–286.

Harmer, R. 2002. The effect of plant competition and simulated summer browsing by deer on tree regeneration. *Journal of Applied Ecology* **38**:1094–1103.

Harmer, R., A. Kiewitt, G. Morgan, and R. Gill. 2010. Does the development of bramble (*Rubus fruticosus* L. agg.) facilitate the growth and establishment of tree seedlings in woodlands by reducing deer browsing damage? *Forestry* **83**:93–102.

Harms, K. E., S. J. Wright, O. Calderón, A. Hernández, and E. A. Herre. 2000. Pervasive

density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**:493–495.

Hartig, F., J. Dyke, T. Hickler, S. I. Higgins, R. B. O'Hara, S. Scheiter, and A. Huth. 2012. Connecting dynamic vegetation models to data - an inverse perspective. *Journal of Biogeography* **39**:2240–2252.

Hättenschwiler, S. 2001. Tree seedling growth in natural deep shade: functional traits related to interspecific variation in response to elevated CO_2. *Oecologia* **129**:31–42.

He, H. S. 2008. Forest landscape models: Definitions, characterization, and classification. *Forest Ecology and Management* **254**:484–498.

Hein, S., C. Collet, C. Ammer, N. L. Goff, J. P. Skovsgaard, and P. Savill. 2009. A review of growth and stand dynamics of *Acer pseudoplatanus* L. in Europe: implications for silviculture. *Forestry* **82**:361–385.

Herrera, C. M., P. Jordano, J. Guitián, and A. Traveset. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *The American Naturalist* **152**:576–594.

Herrera, J. M., J. M. Morales, and D. García. 2011. Differential effects of fruit availability and habitat cover for frugivore-mediated seed dispersal in a heterogeneous landscape. *Journal of Ecology* **99**:1100–1107.

Hickling, R., D. B. Roy, J. K. Hill, and C. D. Thomas. 2005. A northward shift of range margins in British Odonata. *Global Change Biology* **11**:502–506.

Higgins, S. I., R. Nathan, and M. L. Cain. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology* **84**:1945–1956.

Higgins, S. I., and D. M. Richardson. 1999. Predicting plant migration rates in a changing

world: the role of long-distance dispersal. *The American Naturalist* **153**:464–475.

Hille Ris Lambers, J., J. S. Clark, and M. Lavine. 2005. Implications of seed banking for recruitment of Southern Appalachian woody species. *Ecology* **86**:85–95.

Hilton, G. M., and J. R. Packham. 2003. Variation in the masting of common beech (*Fagus sylvatica* L.) in northern Europe over two centuries (1800-2001). *Forestry* **76**:319–328.

Holl, K. D. 2002. Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. *Journal of Ecology* **90**:179–187.

Houle, G. 1999. Mast seeding in *Abies balsamea*, *Acer saccharum* and *Betula alleghaniensis* in an old growth, cold temperate forest of north-eastern North America. *Journal of Ecology* **87**:413–422.

Howe, H. F., and M. N. Miriti. 2004. When seed dispersal matters. *BioScience* **54**:651.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* **13**:201–228.

Hubbell, S., R. Foster, and S. O'Brien. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science* **283**:554–557.

Hyatt, L. A., and A. S. Evans. 1998. Is decreased germination fraction associated with risk of sibling competition? *Oikos* **83**:29.

Ibáñez, I., J. S. Clark, S. LaDeau, and J. H. R. Lambers. 2007. Exploting temporal variability to understand tree recruitment response to climate change. *Ecological Monographs* **77**:163–177.

Inman-Narahari, F., R. Ostertag, S. P. Hubbell, C. P. Giardina, S. Cordell, and L. Sack. 2016. Density-dependent seedling mortality varies with light availability and species abundance in wet and dry Hawaiian forests. *Journal of Ecology* **104**:773–780.

Iverson, L. R., M. W. Schwartz, and A. M. Prasad. 2004. How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography* **13**:209–219.

Jablonski, L. M., X. Wang, and P. S. Curtis. 2002. Plant reproduction under elevated CO_2 conditions: a meta-analysis of reports on 79 crop and wild species. *New Phytologist* **156**:9–26.

Jang, W., C. R. Keyes, and J.-H. Lim. 2013. Application of mathematical models in the spatial analysis of early tree seedling distribution patterns within a treefall gap at Gwangneung Experimental Forest, Korea. *Journal of Plant Biology* **56**:283–289.

Jansen, P. A., M. D. Visser, S. Joseph Wright, G. Rutten, and H. C. Muller-Landau. 2014. Negative density dependence of seed dispersal and seedling recruitment in a Neotropical palm. *Ecology Letters* **17**:1111–1120.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist* **104**:501–528.

Johnson, D. J., W. T. Beaulieu, J. D. Bever, and K. Clay. 2012. Conspecific negative density dependence and forest diversity. *Science* **336**:904–907.

Jones, C. G., R. S. Ostfeld, M. P. Richard, E. M. Schauber, and J. O. Wolff. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. *Science* **279**:1023–6.

Jones, E. W. 1945. *Acer pseudoplatanus* L. *Journal of Ecology* **32**:220–237.

Katul, G. G., A. Porporato, R. Nathan, M. Siqueira, M. B. Soons, D. Poggi, H. S. Horn, and S. A. Levin. 2005. Mechanistic analytical models for long-distance seed dispersal by wind. *The American naturalist* **166**:368–81.

Keane, R. E., P. Morgan, and S. W. Running. 1996, March 1. Fire-BGC: A mechanistic ecological process model for simulating fire succession on coniferous forest landscapes of the northern Rocky Mountains. Forest Service research paper.

Kelly, A. E., and M. L. Goulden. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America* **105**:11823–11826.

Kelly, D. 1994. The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution* **9**:465–470.

Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics* **33**:427–447.

Kirby, K. J., D. R. Bazely, E. A. Goldberg, J. E. Hall, R. Isted, S. C. Perry, and R. C. Thomas. 2014. Changes in the tree and shrub layer of Wytham Woods (Southern England) 1974-2012: Local and national trends compared. *Forestry* **87**:663–673.

Kirschbaum, M. U. F. 2000. Forest growth and species distribution in a changing climate. *Tree Physiology* **20**:309–322.

Klein, E. K., C. Lavigne, and P.-H. Gouyon. 2006. Mixing of propagules from discrete sources at long distance: comparing a dispersal tail to an exponential. *BMC ecology* **6**:3.

Kneeshaw, D. D., R. K. Kobe, K. D. Coates, and C. Messier. 2006. Sapling size influences shade tolerance ranking among southern boreal tree species. *Journal of Ecology* **94**:471–480.

Kobe, R. K. 1999. Light gradient partitioning among tropical tree species through differntial seedling mortality and growth. *Ecology* **80**:187–201.

Kobe, R. K., and K. D. Coates. 1997. Models of sapling mortality as a function of growth to

characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Canadian Journal of Forest Research* **27**:227–236.

Kobe, R. K., S. W. Pacala, J. A. Silander, and C. D. Canham. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications* **5**:517–532.

Koenig, W. D., R. L. Mumme, W. J. Carmen, and M. T. Stanback. 1994. Acorn production by oaks in central coastal California: variation within and among years. *Ecology* **75**:99–109.

Koenig, W., and J. Knops. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. *The American naturalist* **155**:59–69.

Köhler, P., and A. Huth. 1998. The effects of tree species grouping in tropical rainforest modelling: Simulations with the individual-based model Formind. *Ecological Modelling* **109**:301–321.

Krieger, D. J. 2001. Economic value of forest ecosystem services: a review. *The Wildness Society, Washington.DC,USA*.

Krueger, L. M., C. J. Peterson, A. Royo, and W. P. Carson. 2009. Evaluating relationships among tree growth rate, shade tolerance, and browse tolerance following disturbance in an eastern deciduous forest. *Canadian Journal of Forest Research* **39**:2460–2469.

Kunstler, G., D. a. Coomes, and C. D. Canham. 2009. Size-dependence of growth and mortality influence the shade tolerance of trees in a lowland temperate rain forest. *Journal of Ecology* **97**:685–695.

Kuparinen, A. 2006. Mechanistic models for wind dispersal. *Trends in plant science* **11**:296–301.

Ladeau, S. L., and J. S. Clark. 2006. Elevated CO_2 and tree fecundity: the role of tree size,

interannual variability, and population heterogeneity. *Global Change Biology* **12**:822–833.

Lambers, J. H. R., J. S. Clark, and B. Beckage. 2002. Density-dependent mortality and the latitudinal gradient in species diversity. *Nature* **417**:732–735.

Larson, J. E., and J. L. Funk. 2016. Regeneration: an overlooked aspect of trait-based plant community assembly models. *Journal of Ecology* **104**:1284–1298.

Latham, R. E. 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. *Ecology* **73**:2129–2144.

Leishman, M. R. 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos* **93**:294–302.

Lenoir, J., P. A. Marquet, P. De Ruffray, and H. Brisse. 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* **320**:1768–1771.

LePage, P. T., C. D. Canham, K. D. Coates, and P. Bartemucci. 2000. Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. *Canadian Journal of Forest Research* **3**:415-427.

Levin, S., and H. Muller-Landau. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology, Evolution, and Systematics* **34**:575–604.

Liang, M., X. Liu, R. S. Etienne, F. Huang, Y. Wang, and S. Yu. 2015. Arbuscular mycorrhizal fungi counteract the Janzen-Connell effect of soil pathogens. *Ecology* **96**:562–574.

Lichstein, J. W., J. Dushoff, K. Ogle, A. Chen, D. W. Purves, J. P. Caspersen, and S. W.

Pacala. 2010. Unlocking the forest inventory data: relating individual tree performance to unmeasured environmental factors. *Ecological Applications* **20**:684–699.

Lin, J., P. Harcombe, M. Fulton, and R. Hall. 2002. Sapling growth and survivorship as a function of light in a mesic forest of southeast Texas, USA. *Oecologia* **132**:428–435.

Lindner, M., M. Maroschek, S. Netherer, A. Kremer, A. Barbati, J. Garcia-Gonzalo, R. Seidl, S. Delzon, P. Corona, M. Kolström, M. J. Lexer, and M. Marchetti. 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management* **259**:698–709.

Lischke, H., N. E. Zimmermann, J. Bolliger, S. Rickebusch, and T. J. Löffler. 2006. TreeMig: A forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecological Modelling* **199**:409–420.

Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The velocity of climate change. *Nature* **462**:1052–1055.

Long, Z. T., T. H. Pendergast, and W. P. Carson. 2007. The impact of deer on relationships between tree growth and mortality in an old-growth beech-maple forest. *Forest Ecology and Management* **252**:230–238.

Lusk, C. H. 2004. Leaf area and growth of juvenile temperate evergreens in low light: species of contrasting shade tolerance change rank during ontogeny. *Functional Ecology* **18**:820–828.

Martínez, I., and F. González-Taboada. 2009. Seed dispersal patterns in a temperate forest during a mast event: performance of alternative dispersal kernels. *Oecologia* **159**:389–400.

Merow, C., N. LaFleur, J. A. S. Jr., A. M. Wilson, and M. Rubega. 2011. Developing Dynamic Mechanistic Species Distribution Models: Predicting Bird-Mediated Spread of

Invasive Plants across Northeastern North America. *The American Naturalist* **1**:30-43.

Metz, M. R., W. P. Sousa, and R. Valencia. 2010. Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. *Ecology* **91**:3675–3685.

Mihok, B., K. Kenderes, K. J. Kirby, K. Paviour-Smith, and C. A. Elbourn. 2009. Forty-year changes in the canopy and the understorey in Wytham Woods. *Forestry* **82**:515–527.

Mitchell, R. J., J. K. Beaton, P. E. Bellamy, A. Broome, J. Chetcuti, S. Eaton, C. J. Ellis, A. Gimona, R. Harmer, A. J. Hester, R. L. Hewison, N. G. Hodgetts, G. R. Iason, G. Kerr, N. A. Littlewood, S. Newey, J. M. Potts, G. Pozsgai, D. Ray, D. A. Sim, J. A. Stockan, A. F. S. Taylor, and S. Woodward. 2014. Ash dieback in the UK: A review of the ecological and conservation implications and potential management options. *Biological Conservation* **175**:95–109.

Mladenoff, D. J. 2004. LANDIS and forest landscape models. *Ecological Modelling* **180**:7–19.

Moles, A. T., D. S. Falster, M. R. Leishman, and M. Westoby. 2004. Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. *Journal of Ecology* **92**:384–396.

Moles, A. T., and M. Westoby. 2004. What do seedlings die from and what are the implications for evolution of seed size? *Oikos* **106**:193–199.

Moles, A. T., and M. Westoby. 2006. Seed size and plant strategy across the whole life cycle. *Oikos* **113**:91–105.

Monographs, E. 2012. Tolerance to Shade , Drought , and Waterlogging of Temperate Northern Hemisphere Trees and Shrubs. *Ecological Monographs* **76**:521–547.

Moorcroft, P. R. 2006. How close are we to a predictive science of the biosphere? *Trends in Ecology & Evolution* **21**:400–407.

Morecroft, M. D. 2001. Impacts of deer herbivory on ground vegetation at Wytham Woods, central England. *Forestry* **74**:251–257.

Morecroft, M. D., V. J. Stokes, M. E. Taylor, and J. I. L. Morison. 2008. Effects of climate and management history on the distribution and growth of sycamore (*Acer pseudoplatanus* L.) in a southern British woodland in comparison to native competitors. *Forestry* **81**:59–74.

Moustakas, A., and M. R. Evans. 2015. Effects of growth rate, size, and light availability on tree survival across life stages: a demographic analysis accounting for missing values and small sample sizes. *BMC Ecology* **15**:6.

Muller-Landau, H. C., S. J. Wright, O. Calderón, R. Condit, and S. P. Hubbell. 2008. Interspecific variation in primary seed dispersal in a tropical forest. *Journal of Ecology* **96**:653–667.

Myers, J. A., and K. E. Harms. 2009. Seed arrival, ecological filters, and plant species richness: a meta-analysis. *Ecology Letters* **12**:1250–1260.

Nakashizuka, T. 2001. Species coexistence in temperate, mixed deciduous forests. *Trends in Ecology & Evolution* **16**:205–210.

Nanos, N., K. Larson, M. Millerón, and S. Sjöstedt-de Luna. 2010. Inverse modeling for effective dispersal: Do we need tree size to estimate fecundity? *Ecological Modelling* **221**:2415–2424.

Nathan, R. 2006. Long-distance dispersal of plants. *Science* **313**:786–8.

Nathan, R., G. G. Katul, H. S. Horn, S. M. Thomas, R. Oren, R. Avissar, S. W. Pacala, and S.

A. Levin. 2002. Mechanisms of long-distance dispersal of seeds by wind. *Nature* **418**:409–13.

Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* **15**:278–285.

Nathan, R., G. Perry, J. T. Cronin, A. E. Strand, and M. L. Cain. 2003. Methods for estimating long-distance dispersal. *Oikos* **103**:261–273.

Nathan, R., F. M. Schurr, O. Spiegel, O. Steinitz, A. Trakhtenbrot, and A. Tsoar. 2008. Mechanisms of long-distance seed dispersal. *Trends in ecology & evolution* **23**:638–47.

Needham, J., C. Merow, N. Butt, Y. Malhi, T. R. Marthews, M. Morecroft, and S. M. McMahon. 2016. Forest community response to invasive pathogens: the case of ash dieback in a British woodland. *Journal of Ecology* **104**:315–330.

Niinemets, Ü. 1998. Growth of young trees of *Acer platanoides* and *Quercus robur* along a gap-understory continuum : interrelationships between allometry, biomass partitioning, nitrogen, and shade tolerance. *International Journal of Plant Sciences* **159**:318–330.

Normand, S., R. E. Ricklefs, F. Skov, J. Bladt, O. Tackenberg, and J.-C. Svenning. 2011. Postglacial migration supplements climate in determining plant species ranges in Europe. *Proceedings. Biological sciences* **278**:3644–53.

Ogle, K., J. J. Barber, G. A. Barron-Gafford, L. P. Bentley, J. M. Young, T. E. Huxman, M. E. Loik, and D. T. Tissue. 2015. Quantifying ecological memory in plant and ecosystem processes. *Ecology Letters* **18**:221–235.

Van Oijen, M., J. Rougier, and R. Smith. 2005. Bayesian calibration of process-based forest models: bridging the gap between models and data. *Tree Physiology* **25**:915–927.

Overpeck, J. T., D. Rind, and R. Goldberg. 1990. Climate-induced changes in forest disturbance and vegetation. *Nature* **343**:51–53.

Pacala, S. W., C. D. Canham, J. Saponara, J. A. S. Jr., R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* **66**:1–43.

Packham, J. R., P. A. Thomas, M. D. Atkinson, and T. Degen. 2012. Biological flora of the British Isles: Fagus sylvatica. *Journal of Ecology* **100**:1557–1608.

Packham, J., and P. Thomas. 2012. Biological flora of the British Isles: *Fagus sylvatica*. *Journal of Ecology* **100**:1557–1608.

Pagel, J., and F. M. Schurr. 2012. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecology and Biogeography* **21**:293–304.

Parmesan, C. 2006a. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*:667–669.

Parmesan, C. 2006b. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**:637–669.

Patterson, T. M., and D. L. Coelho. 2009. Ecosystem services: Foundations, opportunities, and challenges for the forest products sector. *Forest Ecology and Management* **257**:1637–1646.

Pautasso, M., G. Aas, V. Queloz, and O. Holdenrieder. 2013. European ash (*Fraxinus excelsior*) dieback – A conservation biology challenge. *Biological Conservation* **158**:37–49.

Pearse, I. S., W. D. Koenig, and D. Kelly. 2016. Mechanisms of mast seeding: resources,

weather, cues, and selection. *New Phytologist* **212**:546–562.

Pearson, T. R., D. F. Burslem, C. E. Mullins, and J. W. Dalling. 2002. Germination ecology of neotropical pioneers: interacting effects of environmental conditions and seed size. *Ecology* **83**:2798–2807.

Petritan, A. M., B. Von Lupke, and I. C. Petritan. 2007. Effects of shade on growth and mortality of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings. *Forestry* **80**:397–412.

Petritan, A. M., B. von Lüpke, and I. C. Petritan. 2009. Influence of light availability on growth, leaf morphology and plant architecture of beech (*Fagus sylvatica* L.), maple (*Acer pseudoplatanus* L.) and ash (*Fraxinus excelsior* L.) saplings. *European Journal of Forest Research* **128**:61–74.

Pigot, A. L., and S. R. Leather. 2008. Invertebrate predators drive distance-dependent patterns of seedling mortality in a temperate tree *Acer pseudoplatanus*. *Oikos* **117**:521–530.

Poorter, L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology* **13**:396–410.

Poorter, L. 2007. Are species adapted to their regeneration niche, adult niche, or both? *The American naturalist* **169**:433–42.

Price, D. T., N. E. Zimmermann, P. J. Van Der Meer, M. J. Lexer, P. Leadley, I. T. M. Jorritsma, J. Schaber, D. F. Clark, P. Lasch, S. Mcnulty, J. Wu, and B. Smith. 2001. Regeneration in gap models: Priority issues for studying forest responses to climate change. *Climatic Change* **51**:475–508.

Primack, R. B. 1987. Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics* **18**:409–430.

Quillet, A., C. Peng, and M. Garneau. 2010. Toward dynamic global vegetation models for simulating vegetation–climate interactions and feedbacks: recent developments, limitations, and future challenges. *Environmental Reviews* **18**:333–353.

Reader, R. J., S. . Bonser, T. E. Duralia, and B. D. Bricker. 1995. Interspecific variation in tree seedling establishment in canopy gaps in relation to tree density. *Journal of Vegetation Science* **6**:609–614.

Record, S., R. K. Kobe, C. F. Vriesendorp, and A. O. Finley. 2016. Seedling survival responses to conspecific density, soil nutrients, and irradiance vary with age in a tropical forest. *Ecology* **97**:2406–2415.

Reynolds, J. F., H. Bugmann, and L. F. Pitelka. 2001. How much physiology is needed in forest gap models for simulating long-term vegetation response to global change? Challenges, limitations, and potentials. *Climatic Change* **51**:541–557.

Ribbens, E., J. A. Silander, and S. W. Pacala. 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology* **75**:1794–1806.

Richards, S. A. 2007. Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology* **45**:218–227.

Robledo-Arnuncio, J. J., and C. García. 2007. Estimation of the seed dispersal kernel from exact identification of source plants. *Molecular Ecology* **16**:5098–5109.

Ruiz-Labourdette, D., D. Nogués-Bravo, H. S. Ollero, M. F. Schmitz, and F. D. Pineda. 2012. Forest composition in Mediterranean mountains is projected to shift along the entire elevational gradient under climate change. *Journal of Biogeography* **39**:162–176.

Russo, S. E., P. Brown, S. Tan, and S. J. Davies. 2007. Interspecific demographic trade-offs and soil-related habitat associations of tree species along resource gradients. *Journal of*

Ecology **96**:192–203.

Russo, S. E., S. Portnoy, and C. K. Augspurger. 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology* **87**:3160–3174.

Sala, A., K. Hopping, E. J. B. McIntire, S. Delzon, and E. E. Crone. 2012. Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *New Phytologist* **196**:189–199.

Savill, P. S., C. M. Perrins, D. M. Jones, A. R. Smith, C. W. D. W. D. C. Gibson, K. J. J. Kirby, C. W. D. W. D. C. Gibson, M. D. D. Morecroft, C. W. D. W. D. C. Gibson, C. D. Buesching, J. R. Clarke, S. A. Ellwood, C. King, C. Newman, D. W. Macdonald, N. Fisher, N. D. Brown, C. Hambler, D. J. Rogers, M. D. D. Morecroft, M. E. Taylor, C. M. Perrins, and A. G. Gosler. 2010. Wytham Woods: Oxford's Ecological Laboratory. *Oxford University Press*.

Schimel, D. S. 1995. Terrestrial ecosystems and the carbon cycle. *Global Change Biology* **1**:77–91.

Schnitzer, S. A., and W. P. Carson. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* **82**:913–919.

Schreeg, L. A., R. K. Kobe, and M. B. Walters. 2005. Tree seedling growth, survival, and morphology in response to landscape-level variation in soil resource availability in northern Michigan. *Canadian Journal of Forest Research* **35**:263–273.

Schröter, D., W. Cramer, R. Leemans, I. C. Prentice, M. B. Araújo, N. W. Arnell, A. Bondeau, H. Bugmann, T. R. Carter, C. A. Gracia, A. C. de la Vega-Leinert, M. Erhard, F. Ewert, M. Glendining, J. I. House, S. Kankaanpää, R. J. T. Klein, S. Lavorel, M. Lindner, M. J. Metzger, J. Meyer, T. D. Mitchell, I. Reginster, M. Rounsevell, S. Sabaté, S. Sitch, B. Smith, J. Smith, P. Smith, M. T. Sykes, K. Thonicke, W. Thuiller, G. Tuck,

S. Zaehle, and B. Zierl. 2005. Ecosystem service supply and vulnerability to global change in Europe. *Science* **310**:1333–7.

Schumacher, S., H. Bugmann, and D. J. Mladenoff. 2004. Improving the formulation of tree growth and succession in a spatially explicit landscape model. *Ecological Modelling* **180**:175–194.

Schurr, F. M., O. Steinitz, and R. Nathan. 2008. Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation. *Journal of Ecology* **96**:628–641.

Schwartz, M. W., J. J. Hellmann, J. M. Mclachlan, D. F. Sax, J. O. Borevitz, J. Brennan, A. E. Camacho, G. Ceballos, J. R. Clark, H. Doremus, R. Early, J. R. Etterson, D. Fielder, J. L. Gill, P. Gonzalez, N. Green, L. Hannah, D. W. Jamieson, D. Javeline, B. A. Minteer, J. Odenbaugh, S. Polasky, D. M. Richardson, T. L. Root, H. D. Safford, O. Sala, S. H. Schneider, A. R. Thompson, J. W. Williams, M. Vellend, P. Vitt, and S. Zellmer. 2012. Managed relocation: integrating the scientific, regulatory, and ethical challenges. *BioScience* **62**:732–743.

Sheffer, E., C. D. Canham, J. Kigel, and A. Perevolotsky. 2013. Landscape-scale density-dependent recruitment of oaks in planted forests: More is not always better. *Ecology* **94**:1718–1728.

Shefferson, R. P. 2006. Survival costs of adult dormancy and the confounding influence of size in lady's slipper orchids, genus *Cypripedium*. *Oikos* **115**:253–262.

Shefferson, R. P., J. Proper, S. R. Beissinger, and E. L. Simms. 2003. Life history trade-offs in a rare orchid: The costs of flowering, dormancy, and sprouting. *Ecology* **84**:1199–1206.

Shugart, H. H. 1984. A theory of forest dynamics. The ecological implications of forest

succession models. Page Springer Verlag.

Shugart, H. H., and T. M. Smith. 1996. A review of forest patch models and their application to global change research. *Climatic Change* **34**:131–153.

Silvertown, J. 2004. Plant coexistence and the niche. *Trends in Ecology & Evolution* **19**:605–611.

Sitch, S., B. Smith, I. C. Prentice, A. Arneth, A. Bondeau, W. Cramer, J. O. Kaplan, S. Levis, W. Lucht, M. T. Sykes, K. Thonicke, and S. Venevsky. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology* **9**:161–185.

Snell, R. S., A. Huth, J. E. M. S. Nabel, G. Bocedi, J. M. J. Travis, D. Gravel, H. Bugmann, A. G. Gutiérrez, T. Hickler, S. I. Higgins, B. Reineking, M. Scherstjanoi, N. Zurbriggen, and H. Lischke. 2014. Using dynamic vegetation models to simulate plant range shifts. *Ecography* **37**:1184–1197.

Soons, M. B., G. W. Heil, R. Nathan, and G. G. Katul. 2004. Determinants of long-distance seed dispersal by wind in grasslands. *Ecology* **85**:3056–3068.

Sork, V. L., J. Bramble, and O. Sexton. 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. *Ecology* **74**:528–541.

Stancioiu, P. T., and K. L. O'Hara. 2006. Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania. *European Journal of Forest Research* **125**:151–162.

Steinitz, O., D. Troupin, G. G. Vendramin, and R. Nathan. 2011. Genetic evidence for a Janzen-Connell recruitment pattern in reproductive offspring of *Pinus halepensis* trees. *Molecular Ecology* **20**:4152–4164.

Stoyan, D., and S. Wagner. 2001. Estimating the fruit dispersion of anemochorous forest trees. *Ecological Modelling* **145**:35–47.

Symonds, M. R. E., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology* **65**:13–21.

Tapper, P.-G. 1992a. Irregular fruiting in *Fraxinus excelsior*. *Journal of Vegetation Science* **3**:41–46.

Tapper, P.-G. 1992b. Demography of persistent juveniles in *Fraxinus excelsior*. *Ecography* **15**:385–392.

Taylor, A. R., H. Y. H. Chen, and L. VanDamme. 2009. A review of forest succession models and their suitability for forest management planning. *Forest Science* **55**:23–36.

Thomas, C. D. 2010. Climate, climate change and range boundaries. *Diversity and Distributions* **16**:488–495.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. Townsend Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. *Nature* **427**:145–148.

Thomas, P. A. 2016. Biological flora of the British Isles: Fraxinus excelsior. *Journal of Ecology* **104**:1158–1209.

Thomson, F. J., A. T. Moles, T. D. Auld, and R. T. Kingsford. 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology* **99**:1299–1307.

Thuiller, W., C. Albert, M. B. Araújo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler, G. F. Midgley, J. Paterson, F. M. Schurr, M. T. Sykes, and N. E. Zimmermann. 2008. Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics* **9**:137–152.

Thuiller, W., S. Lavorel, M. B. Araújo, M. T. Sykes, and I. C. Prentice. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America* **102**:8245–50.

Thuiller, W., T. Münkemüller, S. Lavergne, D. Mouillot, N. Mouquet, K. Schiffers, and D. Gravel. 2013. A road map for integrating eco-evolutionary processes into biodiversity models. *Ecology Letters* **16**:94–105.

Tierney, G. L., and T. J. Fahey. 1998. Soil seed bank dynamics of pin cherry in a northern hardwood forest, New Hampshire, U.S.A. *Canadian Journal of Forest Research* **28**:1471–1480.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**:2–16.

Tripler, C. E., C. D. Canham, R. S. Inouye, and J. L. Schnurr. 2005. Competitive hierarchies of temperate tree species: Interactions between resource availability and white-tailed deer. *Écoscience* **12**:494–505.

Tubby, K. V., and J. F. Webber. 2010. Pests and diseases threatening urban trees under a changing climate. *Forestry* **83**:451–459.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* **88**:225–238.

Vacchiano, G., D. Ascoli, F. Berzaghi, M. E. Lucas-Borja, T. Caignard, A. Collalti, P. Mairota, C. Palaghianu, C. P. O. Reyer, T. G. M. Sanders, E. Schermer, T. Wohlgemuth,

and A. Hacket-Pain. 2018. Reproducing reproduction: How to simulate mast seeding in forest models. *Ecological Modelling* **376**:40–53.

Valladares, F., and Ü. Niinemets. 2008. Shade Tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics* **39**:237–257.

Vanhellemont, M., L. Baeten, H. Verbeeck, M. Hermy, and K. Verheyen. 2011. Long-term scenarios of the invasive black cherry in pine-oak forest: Impact of regeneration success. *Acta Oecologica* **37**:203–211.

Vdzquez-Yanes, C., and A. Orozco-Segovia. 1993. Patterns of seed longevity and germination in the tropical rainforest.

Walters, M. B., and P. B. Reich. 1996a. Are Shade Tolerance, Survival, and Growth Linked? Low Light and Nitrogen Effects on Hardwood Seedlings. *Ecology* **77**:841–853.

Walters, M. B., and P. B. Reich. 1996b. Are shade tolerance, survival, and growth sinked? sow Light and nitrogen effects on hardwood seedlings. *Ecology* **77**:841–853.

Walters, M. B., and P. B. Reich. 2014. Seed size , nitrogen supply , and growth rate affect tree seedling survival in deep shade. *Ecology* **81**:1887–1901.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* **416**:389–395.

Wang, B. C., and T. B. Smith. 2002. Closing the seed dispersal loop. *Trends in Ecology & Evolution* **17**:379–386.

Waters, T. L., and P. S. Savill. 1992. Ash and sycamore regeneration and the phenomenon of their alternation. *Forestry* **65**:417–433.

Wenny, D. G., and D. J. Levey. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences of the United States of America* **95**:6204–6207.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**:S120–S139.

Whitmore, T. C. 1989. Canopy gaps and the two major groups of forest trees. *Ecology* **70**:536–538.

Wright, J. S. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* **130**:1–14.

Wright, S. J., K. Kitajima, N. J. B. Kraft, P. B. Reich, I. J. Wright, D. E. Bunker, R. Condit, J. W. Dalling, S. J. Davies, S. Díaz, B. M. J. Engelbrecht, K. E. Harms, S. P. Hubbell, C. O. Marks, M. C. Ruiz-Jaen, C. M. Salvador, and A. E. Zanne. 2010. Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* **91**:3664–3674.

Wyckoff, P. H., and J. S. Clark. 2000. Predicting tree mortality from diameter growth: a comparison of maximum likelihood and Bayesian approaches. *Canadian Journal of Forest Research* **30**:156–167.

Yamamoto, S.-I. 2000. Forest gap dynamics and tree regeneration. *Journal of Forest Research* **5**:223–229.

Yamazaki, M., S. Iwamoto, and K. Seiwa. 2009. Distance- and density-dependent seedling mortality caused by several diseases in eight tree species co-occurring in a temperate forest. *Plant Ecology* **201**:181–196.